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Spatial dynamics of a host-parasitoid community: confronting theory with data

by

Brian H. Van Hezewijk ©

A thesis submitted to the Faculty of Graduate Studies and Research in
partial fulfilment of the requirements for the degree of
Doctor of Philosophy

in

Environmental Biology and Ecology

Department of Biological Sciences

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Dedication

To my parents for the foundations,
to my teachers for the tools, and
to my family for the reason.

Abstract

Inclusion of spatial processes in models of host-parasitoid dynamics offers the potential for explaining patterns of community stability, coexistence of competing species, and self-generating patterns of abundance. There is, however, little empirical evidence to gauge the importance of spatial processes in the dynamics of natural host-parasitoid communities. I studied both local and spatial interactions between the willow pinecone gall midge *Rabdophaga strobiloides*, the plant on which it feeds *Salix bebbiana*, and its two specialist wasp parasitoids, *Gastrancistrus* sp. and *Torymus cecidomyiae*. Spatially referenced census data were collected for each species over four generations and these data were used to parameterise a host-parasitoid model incorporating the local processes of reproduction and mortality and the spatial process of dispersal. Gall diameter was important in determining both the intensity and cause of mortality experienced by the midge while in the gall. Overall, midges survived best in the large galls that provided a refuge from parasitism and predation. By fitting a variety of spatially explicit host-parasitoid models to the census data, I found that midge dispersal was best described by a power function and that the midge tended to disperse less than both parasitoid species. The parasitoid *T. cecidomyiae*, described as the superior larval competitor, dispersed less widely than *Gastrancistrus* sp., the inferior parasitoid. Experimental manipulations and an analysis of colonisation of naturally vacant patches confirmed that the two parasitoid species differ in their dispersal abilities but the observed difference was too small to explain the coexistence of these competitors. In numerical simulations variation in

dispersal patterns between the two parasitoid species had little effect on the amount of host use overlap. Coexistence did depend, however, on both spatial and temporal variability in the average gall diameter among willows. Lower temporal variability or higher spatial variability resulted in a higher probability of the two parasitoid species coexisting. My results suggest that in communities where hosts reside in refuges from parasitism, host-parasitoid dynamics are better described by local processes or spatial variation in refuge quality, than by differences in dispersal rates.

Acknowledgements

It is often the case that any substantial piece of work is the result of the work of many people besides the author. This case is no exception.

I would first like to acknowledge the significant contribution of my supervisor, Dr. Jens Roland. His early suggestion that willow galls may be a useful model system for testing spatial hypotheses turned out to be instrumental in the development of this dissertation. Furthermore, he provided me with a stable, challenging, and enjoyable environment in which to pursue my work. In all respects he has proven to be an exceptional supervisor, colleague, and friend.

I would also like to thank my supervisory committee, Rosemarie DeClerk-Floate, Fiona Schmiegelow, and John Spence, as well as my external examiner Peter Price, for their valuable suggestions and guidance throughout the development of this project and their insightful editing during the writing of this thesis. Subhash Lele in the Department of Mathematics and Statistics, at the University of Alberta provided me with many of the quantitative skills necessary for properly analysing my data.

One of the strengths of this work lies in the volume and quality of the data. This is largely the result of the efforts of Kris Sabourin who collected, measured and dissected more than 10000 galls. Aside from significantly reducing my workload, he also made lab and fieldwork enjoyable and entertaining. Even when faced with the

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This work was conducted at the Rumsey Ecological Reserve in Alberta and as such, I would like to acknowledge the cooperation and assistance of the Alberta Ministry of Agriculture, Food and Rural Development, Public Lands Division. An attractive campsite while working at the reserve was kindly provided by Ducks Unlimited.

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Table of Contents

CHAPTER 1: GENERAL INTRODUCTION 1
  Aspatial models of host-parasitoid dynamics 1
  The development of spatial models 2
  Empirical evidence for the importance of spatial processes 3
  Objectives, general approach, definitions and thesis outline 6
  Natural history of the willow pinecone gall midge and its parasitoids 9
 LITERATURE CITED 12
CHAPTER 2: THE EFFECT OF GALL SIZE ON MORTALITY OF *RABDOPHAGA STROBILOIDES* 20
 INTRODUCTION 20
 METHODS 22
  Life History of *Rabdophaga strobiloides* 22
  Gall collections and measurements 24
  Description of mortality vs. gall size 26
  Estimation of size-dependent marginal attack rates 26
  Variation in gall size among willows and years 28
 RESULTS 29
  Larval mortality 29
  Mortality and gall diameter 30
  Attack rates and gall diameter 32
  Variability in gall diameter 33
 DISCUSSION 34
 LITERATURE CITED 41
CHAPTER 3: DIFFERENTIAL DISPERSAL RATES PREDICT CHAOS IN A NATURAL HOST-PARASITOID COMMUNITY 58
 INTRODUCTION 58
 METHODS 59
  Description of the host-parasitoid-parasitoid community 59
  Description of the study site and census techniques 61
  Dispersal among patches 62
  Within-patch processes 64
  The dispersal-growth model 66
  Model fitting and selection 66
 RESULTS 69
  Spatial and temporal patterns in abundance 69
  Host dispersal 70
  Parasitoid dispersal 70
 DISCUSSION 71
 LITERATURE CITED 76

CHAPTER 4: DYNAMICS OF A HOST-PARASITOID COMMUNITY: THE EFFECTS OF SPATIAL AND TEMPORAL REFUGES ON THE COEXISTENCE OF COMPETING PARASITOID SPECIES 101

INTRODUCTION 101
  Natural history of the host-parasitoid community 104
METHODS 105
  Description of study area and general methods 105
  Assessing competition for hosts between *Gastrancistrus* and *Torymus* 107
  Measuring dispersal 107
    Invasion ability 107
    Patch colonisation ability 109
  Measuring the effect of dispersal on host-use overlap 111
  Assessing the effect of gall-size refuges on coexistence 113
    Temporal variability 113
    Spatial variability 115
RESULTS 117
  Competition for hosts between *Gastrancistrus* and *Torymus* 117
  Dispersal 118
    Invasion ability 118
    Patch colonisation ability 119
  The effect of dispersal on host-use overlap 121
  Refuges and coexistence 122
    Temporal variability 122
    Spatial variability 122
DISCUSSION 123
  How does gall size affect the coexistence of parasitoids? 123
    Can differential dispersal mitigate competition within Rabdophaga galls? ... 124
LITERATURE CITED 128
APPENDIX 4-A 156
  Algorithm for generating serially correlated observations from a sample distribution. 156

CHAPTER 5: GENERAL DISCUSSION AND CONCLUSIONS 158

  The importance of gall size for hosts and parasitoids 159
  Measuring host and parasitoid dispersal 162
  The role of dispersal in the dynamics of the willow pinecone gall community.. 165
  Summary 167
LITERATURE CITED 169

APPENDIX A: IDENTIFYING GALL FATES 175

KEY TO FATES OF *RABDOPHAGA STROBILOIDES* LARVAE 176

List of Tables

Table 1-1 Parasitoids reared from *Rabdophaga strobiloides* galls at the Rumsey Ecological Reserve... 19
Table 2-1 Proportions of galls killed by each mortality source................. 47
Table 2-2 Analysis of variance in gall diameter explained by willow clones.. 48
Table 2-3 Temporal correlation in gall diameter.................................. 49
Table 3-1 Growth-dispersal models for the midge and parasitoids............. 81
Table 3-2 Parameter estimates for the *R. strobiloides* growth-dispersal model.. 82
Table 3-3 Parameter estimates for the *Gastrancistrus* growth-dispersal model.. 83
Table 3-4 Parameter estimates for the *Torymus* growth-dispersal model....... 84
Table 4-1 The effect of landscape on colonisation by *R. strobiloides*........... 134
Table 4-2 The effect of landscape on colonisation by *Gastrancistrus*........... 135
Table 4-3 The effect of landscape on colonisation by *Torymus*.................. 136

List of Figures

Figure 2-1 Distribution of gall diameters ... 51
Figure 2-2 Midge mortality rates as a function of gall diameter ... 53
Figure 2-3 Random multiparasitism by *Torymus* ... 55
Figure 2-4 Estimated attack rates for parasitoids and birds ... 57
Figure 3-1 Aerial photograph of the study area at the Rumsey Ecological Reserve ... 86
Figure 3-2 Graphical representation of the host-parasitoid model with refuges ... 88
Figure 3-3 Susceptibility of midge larvae to parasitoid attack ... 90
Figure 3-4 Sub-sampling scheme to estimate confidence limits for model parameters ... 92
Figure 3-5 Variation in the rate of change in gall numbers among 232 willows ... 94
Figure 3-6 Best fitting dispersal functions for the midge and parasitoids ... 96
Figure 3-7 Growth-dispersal model predictions versus observed data ... 98
Figure 3-8 Simulated population trajectories for the spatially explicit host-parasitoid model ... 100
Figure 4-1 Reference and experimental study areas in the Rumsey Ecological Reserve ... 139
Figure 4-2 Functions describing the susceptibility of galls to parasitism by *Torymus* ... 141
Figure 4-3 Rates of multiparasitism as a function of gall diameter ... 143
Figure 4-4 Abundance of galls as a function of the distance to the edge of the cleared area ... 145
Figure 4-5 Abundance of *Gastrancistrus* as a function of the distance to the edge of the cleared area ... 147
Figure 4-6 Abundance of *Torymus* as a function of the distance to the edge of the cleared area ... 149
Figure 4-7 Simulated rates of multiparasitism versus differences in the dispersal patterns of *Torymus* and *Gastrancistrus* ... 151
Figure 4-8 The effect of temporal correlation in gall diameter on parasitoid coexistence ... 153
Figure 4-9 The effect of spatial variability of refuges on parasitoid coexistence ... 155

Chapter 1:
General Introduction

Aspatial models of host-parasitoid dynamics

The first, and possibly the simplest, explicit formulation of a host-parasitoid model can be attributed to Thompson (1924). He characterised the impact of parasitoid attack on a host population as simply the number of parasitoid eggs laid. Thompson acknowledged that this was clearly an inadequate model for describing the behaviour of parasitoids that could not distinguish previously parasitised hosts and therefore elaborated his model to include the possibility of multiple attacks such that the total impact of a parasitoid population was a decelerating function of the number of parasitoids. In practicality, this model was not much better than the first because it still predicted infinite growth of the host and parasitoid populations or rapid extinction of both (Varley, Gradwell & Hassell 1973).

Nicholson (1933) and Nicholson and Bailey (1935) proposed a similar model involving decelerating parasitoid impact but it was based on a different conceptual foundation; one that hinted at the effect of space. Although Nicholson formulated his models in a completely aspatial manner, he proposed that parasitoids search a limited area of their habitat. With increasing parasitoid density, greater overlap would occur in the areas searched by the individual parasitoids in the population, decreasing their overall efficiency. His models were able to capture the oscillatory dynamics characteristic of many natural host-parasitoid interactions but were too unstable to describe the persistence of hosts and parasitoids, a pattern more common in nature.

The mechanistic nature of Nicholson's models prompted Varley (1947) to develop an empirical model of the interaction between the knapweed gallfly (*Urophora jaceana*) and its parasitoids. This work eventually led to the development of life-table and key factor analysis (Morris 1959, Varley & Gradwell 1971) and highlighted the importance of delayed density-dependence inherent in host-parasitoid interactions. In the decades that followed Varley's detailed study of *Urophora*, research was primarily focused on the role of density-dependence in stabilising host-parasitoid interactions. Holling's (1966) seminal work on the functional responses of predators and parasitoids spurred research into physiological and behavioural mechanisms producing density dependent rates of parasitism (Hassell 1971, Hassell & Rogers 1972).

The common feature of all of the models described above was that they required some form of direct density-dependence to allow persistence of hosts and parasitoids. However, it was becoming clear that in many cases mortality caused by parasitoids was best characterised as either inversely density-dependent or density independent (Varley 1941, Dowden 1961, Eikenbary & Cox 1968, Weseloh 1972,1973).

The development of spatial models

The consideration of dispersal and spatial variation as important processes governing the dynamics of insect populations began with the ideas of Andrewartha & Birch (1954) and den Boer (1968) but Hassell & May (1973) first explicitly formulated these ideas for host-parasitoid communities. Their key finding was that once parasitoids attacked hosts in a spatially non-random manner; *i.e.,* aggregating in areas of high host density, stability of the model could be substantially increased. Later work (Hassell 1984, Chesson & Murdoch 1986, Hassell & May 1988) extended that result to show that both inverse and density-independent patterns of parasitism can also increase stability. These phenomenological spatial models were therefore a substantial improvement in that they could explain the persistence of hosts and multiple species of competing parasitoids under a variety of density dependent patterns.

Based on the theory of non-equilibrium dynamics pioneered by Andrewartha and Birch (1954), den Boer (1968) and Levins (1969), a new class of host-parasitoid models developed with the advent of increased computing power. Hassell, Comins & May (1991) produced a spatially explicit simulation model that demonstrated that regional persistence of hosts and specialist parasitoids in a lattice of identical patches could occur in the presence of completely unstable local interactions. Results from this model showed that a wide array of spatial and temporal dynamics could be produced in response to differing host and parasitoid dispersal rates (Comins, Hassell & May 1992). Further elaborations (Hassell, Comins & May 1994, Comins & Hassell 1996) revealed that coexistence of competing parasitoid species could also result from differential dispersal among species.

Empirical evidence for the importance of spatial processes

There is now a substantial and diverse body of theory concerning the interactions between populations of insect hosts and their parasitoids. Some of this theory (*i.e.*, Nicholson's model and its descendants, and "heterogeneity of risk" models) has been empirically tested (reviewed by Taylor 1990), but spatially explicit metapopulation models of host-parasitoid dynamics have received little attention.

Pimental, Nagel and Madden (1963), following the pioneering work of Huffaker (1958) on spatial dynamics of a mite predator-prey system, were the first to conduct detailed laboratory studies on the dynamics of a host-parasitoid community in a subdivided habitat. They found that increasing the number of subpopulations from 1 to 16 to 30, increased the persistence of the over-all community from under five generations to more than 40. This result could be explained by higher overall population sizes but they also determined that manipulating the parasitoid dispersal rate, while keeping the number of subpopulations constant, also affected persistence. These experiments were designed to examine the effect of host and parasitoid evolution and as such, the data were not interpreted in the context of the limited spatial theory that existed at that time.

In a more recent study of a natural host-parasitoid community in California, (Brodmann, Wilcox & Harrison 1997, Maron & Harrison 1997), there is compelling evidence that differences in host and parasitoid dispersal rates play an important role in the development of stable spatial patterns in host abundance. Furthermore, the data agree well with predictions from a range of spatially explicit host-parasitoid models

(Wilson *et al.* 1999). However, the existence of stable patterns depend critically on very short-range dispersal of the host (*i.e.*, flightless female moths in this case), and long-range dispersal of the parasitoids.

Lei & Hanski (1997, 1998) and more recently van Nouhuys & Hanski (in press), have studied the large-scale metapopulation dynamics of a butterfly and its two specialist parasitoid species. The butterfly, *Melitaea cinxia*, exists as a classic metapopulation with frequent local extinction and colonisation events (Hanski, Kuussaari & Nieminen 1994). There is evidence from these studies that the two parasitoid species have different dispersal rates, and consequently perceive the distribution of hosts in different ways. Roland & Taylor (1997) make a similar claim that the species of parasitoids attacking the forest tent caterpillar interact with their host at different spatial scales, and that these scales correspond to their range of dispersal.

Amarasekare (2000a, 2000b) experimentally tested the hypothesis that differential dispersal allows coexistence of competing parasitoids against the alternative hypothesis that coexistence is maintained by the local host-parasitoid interactions. She found no support for the former and concluded that variation in host productivity was the most important factor governing parasitoid abundance and distribution. Conversely, Briggs & Latto (2000) found that the among-patch dispersal of parasitoids tended to synchronise host population cycles and maintain parasitoid diversity at the patch scale.

Objectives, general approach, definitions and thesis outline

This thesis is an empirical study of how local and spatial processes, and their interaction, affect the population dynamics of species in a host-parasitoid community. The general approach I use is to collect multi-generation, spatially referenced population data on each of the dominant insect species in the community. I then develop and parameterise mechanistic models describing these data by using a combination of experimental and observational (statistical) methods. Through numerical simulations, I use the parameterised models to evaluate the relative roles of local and spatial processes in explaining the abundance of species in the community. I feel that the great advantage of this approach lies in the intimate relationship between field data, biologically realistic models, and established theory.

In this thesis I studied populations of three insect species; the willow pinecone gall midge *Rabdophaga strobiloides* (Osten Sacken) (Diptera: Cecidomyiidae) and its two specialist parasitoids, *Torymus cecidomyiae* (Walker) (Hymenoptera: Torymidae), and *Gastrancistrus* sp. (Hymenoptera, Pteromalidae). This host-parasitoid community is especially amenable to the study of local and spatial processes for many reasons. First, in the area I chose for study, the midge forms galls on a single species of willow that exist as discrete patches on the landscape. Second, the galls formed by the midge are persistent on the willow twigs and are easily censused during the winter months after the willow leaves have dropped. Because population densities are generally low (< 100 galls per hectare), the populations of hosts and parasitoids can be completely enumerated with high precision over a relatively large area. Furthermore, densities can be easily manipulated over varying spatial extents. Lastly, because the galls provide a durable record of the fate of each host and parasitoid, populations can be censused by sampling galls after the insects have emerged thus eliminating the problem of altering densities through destructive sampling.

Throughout this thesis several terms will be used that presently require definition. Although the gall-forming midge, *R. strobiloides,* is parasitic on the willow plants, it is considered here to be the 'host' in order to agree with the typical usage in the insect population dynamics literature. Both *T. cecidomyiae* and *Gastrancistrus* sp. are 'parasitoids' and these, in combination with the host, form a 'host-parasitoid community'. A 'patch' is considered to be one or more stems of *S. bebbiana* that appear to originate from the same rootstock and a 'local population' is defined as all the insects of a given species within the galls in a patch. This definition is perhaps more arbitrary but certainly more operational than the more restrictive definition proposed by Taylor (1990) who considers a local population to be the unit "...within which occur interactions – reproduction, population regulation, predation – and within which most movement is confined". In practice, using such a definition in the context of describing a community of insects necessitates a level of information well above that which is usually available for natural systems. Furthermore, including population regulation as a defining characteristic precludes any possibility of non-equilibrium dynamics at the patch scale, a feature thought to be common in host-parasitoid interactions (Price 1980). A 'patch network' is considered synonymous with 'metapopulation' and describes the collection of patches (that possibly contain local populations) in a given area. The term 'dispersal' is used in this work to describe the sum of all movements of a female insect leading to the displacement of her progeny from her natal location. Traditionally, dispersal is thought to be distinct from the trivial movements associated with foraging activities but in the case of many insects, especially parasitoids, foraging movements are usually associated with the distribution of progeny and not with the accumulation of resources for the adult.

To determine how local and spatial processes affect the dynamics of this host-parasitoid community, a well-structured and appropriately parameterised model is required. To develop this model I first needed to answer some preliminary questions. In Chapter 2, I ask what are the major mortality factors experienced by the host and parasitoids within the gall and how can these mortality factors be predicted? The answers to these questions are used to model the population processes at the patch level. After accounting for local dynamics, I ask in Chapter 3 to what extent are the local populations on neighbouring patches linked by dispersal. I answer this question by developing and parameterising a spatially explicit host-parasitoid model that incorporates local processes and dispersal between patches. In Chapter 4, I describe a large-scale perturbation experiment as well as statistical analyses of patch colonisation events undertaken to determine how landscape heterogeneity affects the dispersal rates of the gall midge and its parasitoids. I then extend the parameterised model developed in Chapter 3 to answer several questions relating to the dynamics of the community. First, can competition between *Torymus* and *Gastrancistrus* parasitoids be moderated by differential dispersal? Second, how does variability among patches, caused by varying gall sizes, affect the coexistence of parasitoids in the community? Lastly, how does spatial and temporal variability in gall size interact with dispersal to affect the coexistence of parasitoids and the stability of the host-parasitoid community?

Natural history of the willow pinecone gall midge and its parasitoids

The willow pinecone gall midge, *R. strobiloides*, has a transcontinental distribution in North America and forms pinecone shaped galls on the terminal buds of several willow species (Gagné 1989). The characteristic pinecone shaped gall was first described by Osten Sacken (1862) but he attributed its formation to the inquiline *Dasineura albovittata* Walsh (Diptera: Cecidomyiidae). The adult midge, larva, and pupa were later described by Walsh (1864) and correctly associated with the gall. Studying populations in the vicinity of Toronto, Ontario, Canada, Brodie (1909) reported that the galls were formed exclusively on *Salix humilis* and that the univoltine adults emerged in early May. He found that two unidentified but clearly distinguishable species of *Torymus* commonly emerged from intact galls. Judd (1953) presented a more careful and comprehensive treatment of the insects found within the galls of *R. strobiloides* collected near London, Ontario, Canada. By separating the central chamber from the rest of the gall he was able to definitively associate three parasitoids with *R. strobiloides*: *T. cecidomyiae*, *Gastrancistrus* sp. (=*Tridymus* sp.), and *Copidosoma* sp. (Hymenoptera: Encyrtidae). Wilson (1968) provided the most recent study on the natural history of this midge. He found galls occurring on *S. eriocephala* Michx. (=*cordata*) in Michigan and reported detailed size and phenology measurements of each of the insect stages as well as gall morphology. Wilson, the only author to report on population size, states that galls "numbered in the thousands" in 1963-64 but were "scarce" in 1965-67.

At my study site in Alberta, Canada, the dominant host for *R. strobiloides* is Bebb's willow (*S. bebbiana* Sarg.). Adult midges emerge synchronously from galls in mid to late May. Females mate within hours of emergence and lay eggs singly on the lower surface of leaves on expanding terminal shoots. Eggs hatch within 2-3 days, after which the first instar larva crawls to the apical meristem and begins feeding. The slight swelling of the developing monothalamous gall can be detected within several weeks. Gall diameter increases throughout the summer (June – September) during which time the larvae pass through three instars. In the fall, larvae spin a thin silk lining (Gagné 1989) on the walls of the central chamber in which they over-winter. Pupation occurs the following spring.

R. strobiloides larvae are attacked by five species of parasitoids at the Alberta sites (Table 1). However, in the area where most of the work for this thesis was undertaken, the majority of parasitism (93%) was caused by *Gastrancistrus* sp. and by *T. cecidomyiae*. Therefore, throughout this thesis, only these two species of parasitoids are studied in detail.

Adult female *Gastrancistrus* sp. emerge from the previous generation of galls in June and attack very young galls containing first instar midge larvae. These solitary koinobionts oviposit through the gall tissues and lay a single egg within the host larva. After hatching, the mandibulate first instar parasitoid larvae kill conspecifics within the host. The surviving larva then moults and spends the remainder of the summer and following winter as an amandibulate second instar in the host larva. Parasitoid development resumes within the mature midge larva in late April, and the parasitoid pupates in mid to late May.

Adults of the solitary idiobiont, *T. cecidomyiae,* emerge from the previous year's galls in early August and attack the current year's galls when the galls have nearly reached their maximum size. At this time the *R. strobiloides* larvae are moulting into their third and final instar. Female parasitoids use their long ovipositor to deposit a single egg on the midge larva or in the larval chamber. The egg hatches within a few days and the parasitoid larva feeds externally on the host, usually moulting once before spending the winter in its second instar. Feeding resumes the following April with the larva moulting into the third instar in May and consuming the remainder of the host. The parasitoid then remains in the chamber as a fully formed larva until mid-July when it pupates.

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Table 1-1: Numbers and relative abundances of five species of parasitoids reared from *Rabdophaga strobiloides* galls at the Rumsey Ecological Reserve in central Alberta, Canada.

Parasitoid	Number recorded	Percent of Total
Torymus cecidomyieae (Walker)	2630	63.7
Torymus nr. *rudbeckiae* Ashmead.	25*	0.6
Gastrancistrus sp.	1219	29.6
Unidentified Platygasteridae	244	5.9
Unidentified Encyrtidae	10	0.2
Total	4128	100

* This value was estimated based on the finding of 2 female specimens of this species in a sample of 215 female *Torymus*.

Chapter 2:
The effect of gall size on mortality of *Rabdophaga strobiloides*

INTRODUCTION

Variation in survival among individuals or "heterogeneity of risk" has been recognised as an important component in stabilising the dynamics of host-parasitoid models (Chesson & Murdoch 1986, Pacala, Hassell & May 1990, Pacala & Hassell 1991). Due to the underlying stochastic nature of models incorporating heterogeneity of risk, 'probabilistic refuges' are created such that some patches of hosts suffer less intense attack than do others. This class of models seems to have grown from earlier work on the stabilising effects of more explicit spatial and structural refuges (Gause 1934, Huffaker 1958, Hassell & May 1973, Hassell 1978). How this variation in vulnerability affects host population stability depends however, on such details as the size or proportionality of the refuge, and the shape of the statistical distribution used to describe survival probabilities (Hassell 1978).

In the context of spatial population dynamics theory, refuges are often represented by homogenous patches of hosts that experience reduced probability of parasitism relative to other patches (Chesson & Murdoch 1986, Pacala *et al.*, 1990). In nature though, patches can be composed of individuals with a wide range and unknown distribution of susceptibilities to parasitism or predation. In addition to qualities of the patch *per se*, such as size or shape, it is this variability among individuals that must be characterised in order to quantify differences in susceptibility among patches.

Gall-forming insects and their natural enemies have played an important role in testing general theories in population dynamics (Varley 1947, Price *et al.* 1995, Dempster *et al.* 1995a, 1995b, Ehler & Kinsey 1995, Latto & Briggs 1995, Briggs & Latto 2000, Briggs & Latto 2001). These communities are typically used because they are often composed of a small number of specialist species (Hawkins & Gagné 1989) and well described by the simplified structure of theoretical models. These studies though, have largely ignored the effect that variation in susceptibility of individual galls has on patch-level heterogeneity, despite the fact that in many cases it has been shown that variation in gall size, morphology or toughness is a good predictor of mortality risk (Weis *et al.* 1985, Craig, Itami & Price 1990, Plakidas & Weis 1994, Redfearn & Cameron 1994, Plantard & Hochberg 1998).

In this part of a larger study of the population dynamics of the willow pinecone gall midge, *Rabdophaga strobiloides* (Osten Sacken) (Cecidomyiidae), I address three fundamental objectives. First, I identify the major sources of mortality for this midge while in the gall and describe the general patterns of mortality over time. Second, I describe the relationship between each source of mortality and gall size to identify patterns and mechanisms of mortality at the smallest possible scale. Third, I elucidate the interactions among these sequential mortality sources by identifying otherwise unobservable patterns of attack based on readily observable patterns of mortality. Meeting these objectives permits an accurate characterisation of patch-level heterogeneity of risk leading to a more explicit study of the spatial dynamics of this community.

METHODS

Life History of *Rabdophaga strobiloides*

Rabdophaga strobiloides is a bud-galling midge with a transcontinental distribution in North America. Wilson (1968) provided an account of the life cycle of this midge in Michigan populations where it forms galls predominantly on the heart-leafed willow, *Salix eriocephela* Michx. At my study site in Alberta, Canada, the dominant host for the midge is Bebb's willow, *S. bebbiana* Sarg.

Adult midges emerge synchronously from galls in mid to late May. Females are mated within hours of emergence and lay eggs singly on the lower surface of leaves on expanding terminal shoots. Egg hatch occurs within 2-3 days, after which the first instar larva migrates to the apical meristem and begins feeding. The slight swelling of the developing monothalamous gall can be detected within several weeks. Gall diameter increases throughout the summer (June – September) in a sigmoidal pattern (Weis & Kapelinski 1984) during which time the larvae pass through three instars. At my study site, final gall diameters range from 2.8 mm to 29.7 mm (mean = 13.84, $n = 7184$). In the fall, larvae spin a thin silk lining on the walls of the central chamber in which they over-winter. Pupation occurs the following spring.

In Alberta, *R. strobiloides* larvae are commonly attacked by two species of parasitoids. Adult female *Gastrancistrus* sp. (Hymenoptera: Pteromalidae) emerge from the previous generation of galls in June and attack very small galls containing first instar midge larvae. These solitary koinobionts oviposit through the gall tissue and lay a single egg within the host larva. After hatching the mandibulate first instar larvae kill conspecifics within the host. The surviving larva then moults and spends the remainder of the summer and following winter as an amandibulate second instar in the dormant host larva. Parasitoid development resumes within the mature midge larva in late April, and the parasitoid pupates in mid to late May.

Galls are also parasitised by *Torymus cecidomyiae* (Walker) (=*strobiloides*) (Hymenoptera: Torymidae) later in the season. This solitary idiobiont emerges from the previous year's galls in early August and attacks the current year's galls when they have nearly reached their final size. At this time the host larvae are moulting into their third and final instar. Female parasitoids use their long ovipositor to deposit a single egg on the midge larva or in the larval chamber. The egg hatches within a few days and the parasitoid larva feeds externally on the host usually moulting once before spending the winter in its second instar. Because *Torymus* larvae will also feed on *Gastrancistrus* larvae already present within the host, they could be classified as facultative hyperparasitoids (*sensu* Godfray 1994). Feeding resumes the following April with the larva moulting into the third instar in May and consuming the remainder of the host. The parasitoid then remains in the chamber as a fully formed larva until mid-July when it pupates.

Winter predation is a third major source of mortality that midges experience as larvae in the galls. Although predation has not been observed, it is suspected to be caused by chickadees (*Poecilies* sp.) based on the type of damage to the galls and because black-capped chickadees (*P. atricapillus*) are common in the area during the winter months (personal observation) and have been recorded feeding on other galling insects (Uhler 1951, Cane & Kurczewski 1976, Schlicter 1978).

In some cases a specific mortality cannot be assigned to a midge because: a) the larva in the central chamber has decomposed to an unidentifiable state, b) death occurred before or during the second instar and a larval chamber had not yet formed, or c) an unidentified lepidopteran larva had fed excessively on gall tissue destroying the central chamber. In each of these cases mortality was classified as 'Other' with secondary classification as 'fungus', 'failed', and 'leps' respectively. In contrast to the other forms of mortality, this group of causes seems to result in the premature death of the larva, either in the first or second instar, and often results in malformed galls.

Gall collections and measurements

As part of a larger study on the spatial dynamics of the midge and its parasitoids, a complete census of galls was made in a 30-hectare site at the Rumsey Ecological Reserve, Alberta, Canada (51°55'N, 112°38W). The vegetation in the reserve is dominated by fescue prairie grassland composed mainly of *Festuca hallii* (Vasey) Piper, *Stipa* spp. and *Agropyron* spp., with patches of *Populus tremuloides* Michx., *Salix* spp. and *Rosa* spp. (Strong & Leggat 1992). The most common species of willows are *Salix petiolaris* J.E. Smith and *S. bebbianna*, but galls have never been found on the former species at this study site.

All the galls on each of 388 willows in the study area were censused each year from 1997 through 1999. In 1997 it was also possible to census the 1996 generation because galls persist on the twigs for several years and because each generation of galls is distinguishable on the bases of ageing and drying of the galls. In April 1998 I removed all of the galls in the 30 ha area. This collection served two purposes. First, it provided census data for both the 1996 and 1997 cohort of galls. Second, because no insects had yet vacated the 1997 galls, it created a relatively large area devoid of both hosts and parasitoids. This was done as part of a separate study on the dispersal of hosts and parasitoids (Chapter 3). In November 1999, two summers after the removal in the spring of 1998, galls from the invading 1998-generation and the subsequent 1999-generation were also collected. It is important to note that because the 1999-generation was collected in the fall while all insects were still within the galls, this cohort was not exposed to winter predation by birds.

The minimum diameter of each gall at its widest point was measured to the nearest millimetre using callipers. Gall fates were determined by dissection using a binocular microscope to examine the contents of the central chamber. In some years (1996, 1998), collections were made after the insects had vacated the galls. In these cases fates were determined using features of the vacant gall characteristic of each source of mortality (Appendix A).

In the *R. strobiloides* community, winter predation by birds masks all preceding parasitism events. Similarly, parasitism by the ectoparasitoid, *T. cecidomyiae* is thought to mask earlier parasitism by *Gastrancistrus*. To correct for the effects of these sequential mortalities and thus to estimate true rates of attack for each, a random subset of the 1999 generation of galls were dissected before either parasitoid species had completed its second stadium (recall that they were collected before winter predation). This allowed an unbiased enumeration of both parasitoid species because at this stage it was possible to determine if a host was multiply parasitised.

Description of mortality vs. gall size

In all cases generalised additive models (GAM; Hastie & Tibshirani 1990) were used to describe the effect of gall diameter on survival from each mortality factor. This was done for two reasons: first, because this class of models allows binary response data (survived, died) each gall could be used as an individual replicate avoiding the loss of information caused by pooling galls into diameter classes, and second, because I had no expectations of the shape of the survival functions, and cubic splines could be used to describe any non-linear relationships between survival and gall diameter (Schluter 1988).

Estimation of size-dependent marginal attack rates

Given the size-dependent attack rates and the subsequent size-dependent rates of host mortality resulting from successful attacks, the difference between these two rates would estimate the mortality experienced by one natural enemy as a result of contemporaneous attacks by another natural enemy. In most years galls were collected at the end of the season and I was therefore only able to directly measure successful parasitism and predation rates. Using methods similar to those proposed by Royama (1981), I estimated the unobserved attack rates for each natural enemy and each 1 mm gall size class, based on the assumption that bird attacks are independent of parasitism and always kill the host or parasitoid in the gall, and on the assumption that *T. cecidomyiae* and *Gastrancistrus* attacks are independent of each other. I tested this second assumption by dissecting a subset of the 1999 galls collected before parasitoid larval development was complete (henceforth the pre-development sample). I compared observed rates of multiparasitism in these galls to those predicted assuming random overlap in parasitism by the two species. Predictions were made separately for each diameter class to control for possible differences in the size preferences of the two parasitoid species. These same data also allowed me to determine the frequency with which *T. cecidomyiae* larvae (*i.e.*, the later attacking species) win in interactions with *Gastrancistrus* larvae. To do this I, compared the observed frequencies of parasitism for each species from a pre-development sample of galls (see above) to the frequencies of parasitism from dissections conducted after parasitoids had matured (post-development sample).

Given the above assumptions the attack rates of each species can be calculated using the following system of equations solved by iteration:

$$B_a = B_p \qquad (1)$$

$$T_a = T_p / (1 - B_a - (1 - B_a)(1 - T_s)G_a) \quad (2)$$

$$G_a = G_p / (1 - B_a - T_s T_a (1 - B_a)) \quad (3)$$

where and B_a and B_p represent the attack and predation rates of birds, T_a and T_p represent the estimated attack rate and the observed parasitism rates of *T. cecidomyiae*, T_s represents the survival rate of *T. cecidomyiae* when attacking galls parasitised by *Gastrancistrus*, and G_a and G_p represent the estimated attack rate and the observed parasitism rate of *Gastrancistrus*. Equation 1 simply states that the bird attack rate is equal to the observed bird predation rate assuming that attacks by birds are not obscured by any other mortality factor. In equation 2, the *Torymus* attack rate is estimated by inflating the predation rate by an amount proportional to the fraction of attacks which are obscured by either bird attacks (B_a) or *Gastrancistrus* attacks that resulted in successful parasitism ($(1-T_s)G_a$). Lastly, in equation 3, the number of *Gastrancistrus* attacks are similarly estimated by inflating the observed parasitism rate by an amount proportional to the fraction of attacks which are obscured by either bird attacks (B_a) or successful *Torymus* attacks (T_sT_a).

Variation in gall size among willows and years

To estimate the effect that willow phenotype has on the size of galls I analysed the variation in gall diameters using willow clone as the random factor in a model-II ANOVA. Estimates of the variance components were calculated using the 'varcomp' function in S-plus 2000 with estimation based restricted maximum likelihood. Effects were estimated separately for each year. Temporal variability in gall size was described using Pearson's correlation coefficient calculated among pairs of years, using willows as replicates.

RESULTS

Larval mortality

In each year the distribution of gall diameters was approximately bell shaped with truncated tails (Fig. 2-1) and was similar among years with a few subtle differences. In 1997 and 1999 average gall size tended to be smaller than in 1996 and 1998. This was due to a skewing toward small galls rather than an even shift in the distributions. In 1997 and 1999 the percentage of galls less than 14 mm was 58% and 60% compared to 47% in both 1996 and 1998.

In all years there is a substantial overall increase in midge survival with increasing gall diameter (Fig. 2-1). In 1999, the survival within the small galls was better due to the lack of bird predation on our sample. In 1997 and 1998 there was an indication of decreased survival among the largest galls but even with the large overall sample sizes there were very few galls in these size classes.

The proportion of midges that were killed by 'other' causes varied little between years (Table 2-1). In all years, approximately half of the midges dying from 'other' causes did so in the first instar and were classified as 'failed' because a larval chamber had not yet developed. Most of the remaining larval deaths in the 'other' category were attributed to lepidopteran feeding damage and to fungal infections. The proportion of galls successfully parasitised by *Gastrancistrus* was low in the first two years but increased substantially in the first year after removal (1998), and was higher still in the year after that (1999). The proportion of galls parasitised by *T. cecidomyiae* was moderate in 1996 and 1997, two years preceding gall removal, declined in 1998 one generation after removal, and was high again in 1999. Bird predation was low in 1996, moderate in 1997, high in 1998, and then very low in 1999. Observed rates of bird predation in 1999 were biased low because galls were collected in December before the majority of bird foraging had occurred.

Mortality and gall diameter

In general, mortality due to 'other' causes decreased with increasing gall diameter (Fig. 2-2). With the exception of small galls in 1996, the pattern of mortality due to 'other' causes was remarkably similar among years.

In the years prior to the gall removal experiment, rates of successful parasitism by *Gastrancistrus* were generally low (Table 2-1, Fig. 2-2). In 1996 the highest rates of parasitism were in galls 15-20 mm in diameter and in 1997 parasitism rates appeared to increase linearly with increasing gall diameter. In 1998, the generation following gall removal, the total parasitism rate rose approximately three-fold and still showed increased parasitism with increasing gall diameter. In 1999, observed parasitism rates were higher still, especially among smaller galls. This was likely due to the near absence of bird predation in these samples (due to fall gall collections) that would normally obscure many parasitoid attacks.

Over the four years of sampling there was substantial variation in the overall proportion of galls parasitised by *T. cecidomyiae* (Table 2-1). Parasitism rates remained nearly constant in 1996 and 1997, decreased three-fold in 1998, one generation following removal, and were highest in 1999. Interestingly, there was very little variation among years in the shape of the curves describing *Torymus* parasitism as a function of gall size. On average, the maximum parasitism rates were on galls 12.8 mm in diameter (range = 12.4 to 13.4 mm) and parasitism declined with either increasing or decreasing gall diameter.

In examining patterns of bird predation with respect to gall diameter there is a suspected bias in the 1996 data. Unlike the other years, the 1996 cohort of galls remained on bushes for two consecutive winters. In the first winter the twigs on which galls form remain green and do not break easily (personal observation). During the second summer these twigs senesce and become brittle. In the subsequent winter, galls that are attacked by birds are probably more likely to fall to the ground during attack thus creating a bias in the data set. For this reason, I focus my analysis and interpretation on the years 1997, 1998 and 1999, although the 1996 data are included for completeness. Two important patterns are evident in the data for the years 1997-1999 (Table 2-1, Fig. 2-2). First, the overall bird predation rate increases between 1997 and 1998. As noted earlier, the low predation rate in 1999 is due to the collection of galls before most bird predation would have occurred. Second, the shapes of the smoothed functions remain relatively constant between years but their locations shift toward larger gall sizes from 1997 to 1999. This indicates an increase in the average size of galls attacked by birds despite a relatively constant distribution of gall sizes among years.

Attack rates and gall diameter

As noted above, midges dying from 'other' causes tended to die earlier in development than from parasitism or predation. I assumed that parasitism or predation later in the season did not mask any mortality from these sources. Therefore, I assume that 'attack' rates are identical to observed mortality rates for this class of causes.

Direct measurements of attack rates using the 1999 pre-development sample of galls (see 'Estimation of size-dependent marginal attack rates' in methods), validated my assumption of random overlap in parasitism for *Gastrancistrus* and *T. cecidomyiae* (Fig. 2-3). When I compared the observed rates of multiparasitism to those predicted based on the marginal attack rates for each species, the slope of the regression line was approximately one, as would be expected under the random attack hypothesis. In the pre-development sample of 656 parasitised galls, 38.2% were attacked by *Gastrancistrus* alone, 42.6% by *T. cecidomyiae* alone, and 19.2% by both species. In the post-development sample of 1286 parasitised galls, 29.9% were parasitised by *Gastrancistrus*, and 70.1% by *T. cecidomyiae.* Therefore, the most parsimonious explanation for this pattern of parasitism is 100% survival of *T. cecidomyiae* in multiply parasitised hosts.

I calculated diameter-dependent attack rates for *Gastrancistrus* sp. for each year using the result of random overlap in parasitism and an 100% competitive dominance of *T. cecidomyiae*, and by assuming that the probability of bird predation does not depend on gall contents (Fig. 2-4). In all years, diameter-dependent attack rates by *Gastrancistrus* increased with increasing gall diameter; attack rates did not differ substantially from the corresponding parasitism rates. In 1996 and 1997 mortality of larval *Gastrancistrus* was approximately 40% in galls less than 15 mm and was caused by both *T. cecidomyiae* parasitism and bird predation in nearly equal amounts. Mortality of *Gastrancistrus* sp. decreased dramatically with increasing gall diameter over 15 mm. In 1998 and 1999, the mortality of larval parasitoids was dominated by bird predation and *T. cecidomyiae* parasitism respectively. Over the range of gall sizes which *Gastrancistrus* sp. attack most often (12 - 22 mm), mortality again decreased sharply with increasing diameter as it did in 1996 and 1997.

In general, estimated attack rates for *T. cecidomyiae* did not differ substantially from observed parasitism rates (Fig. 2-4). This was due to low rates of overlap in gall selection by *T. cecidomyiae* and by birds, the highest mortality factor during larval *T. cecidomyiae* development. However, in 1998 when birds attacked galls larger than usual, an estimated 31% of larval *T. cecidomyiae* were subsequently preyed on compared to 5% and 11% in 1996 and 1997.

Variability in gall diameter

I found that in the four cohorts of galls (1996 - 1999 inclusive), approximately a third of the variation in gall size could be explained by the willow clone factor (Table 2-2) and that this proportion was relatively constant over time. Similarly, gall size within willows was significantly correlated between years at lags of 1-3 years (Table 2-3). Because all of the insects in the 1997 cohort were removed from the area, the correlation in gall size between 1997 and 1998 must be due to factors associated with particular willows and not by factors associated with the families of gall midges inhabiting a particular willow.

DISCUSSION

The relationships among gall size, attack rates, and larval mortality are striking in their consistency among years for each mortality factor, and for the differences among mortality factors. Although inferring process from pattern can be risky, I believe that the robust patterns of mortality seen in this community suggest that specific mechanisms underlie each relationship. Furthermore, in the case of the two parasitoid species, the change in pattern among years are best interpreted as resulting from interactions between mortality factors. These interactions may have important population dynamic and evolutionary consequences but also allow for a robust characterisation of susceptibility at the scale of individual hosts.

Galls dying from 'other' causes stand apart from other mortality factors because it is likely that this factor affects gall size rather than being affected by it. Galls that fail early in development (the majority of cases, Table 2-1), stop growing and consequently have small final diameters. Because gall diameter growth is sigmoidal (Weis & Kapelinski, 1984), a constant gall failure rate produces an expected relationship in which the proportion of galls dying from 'other' causes is greatest in the smallest diameter classes. This is consistent with the observed patterns (Fig. 2-2, top row).

For *Gastrancistrus*, the attack rate and the mortality rate both increase with increasing gall diameter. The obvious advantage of this pattern of attack for *Gastrancistrus* is the avoidance of a high risk of mortality from *T. cecidomyiae* and birds, which commonly attack medium and small-sized galls respectively. Although this relegates *Gastrancistrus* to a small proportion of the total available hosts, it also means that large galls provide a nearly complete refuge for this parasitoid. However, this species attacks hosts early in the season when galls are only barely discernible swellings. How, or even if females can detect those hosts that will eventually produce large galls is unknown. An alternative explanation for parasitism of larger galls is that females attack galls at random, and that parasitised hosts are stimulated in some way to produce larger galls. In several cases, it has been shown that endoparasitoids induce their hosts to prolong larval feeding (Thorpe 1933) or induce supernumerary larval instars (Beckage 1985). If gall size is linked to the duration or intensity of feeding in *R. strobiloides* then this mechanism would result in more *Gastrancistrus* sp. larvae escaping subsequent predation by other natural enemies and thereby improving its own fitness.

The pattern of attack for *T. cecidomyiae* seems to be shaped by two separate processes. First, large galls are probably not attacked due to limitations on ovipositor length, a phenomenon common in other *Torymus* species attacking galls (Romstöck-Völkl 1990, Redfern & Cameron 1994, Plantard & Hochberg 1998). The eggs of this ectoparasitoid must be laid directly on the host or in the host larval chamber for the parasitoid larva to successfully establish. Laboratory observations of oviposition attempts (B. Van Hezewijk, unpublished data) suggest that when galls are greater than 18 mm in diameter there is a less than 1% chance of successful oviposition compared with galls 12 mm in diameter which experience a 29% oviposition rate.

There are several explanations for why small galls are infrequently attacked by *T. cecidomyiae*. First, small galls may be more difficult to find by searching parasitoids. This seems unlikely, however, based on the results of the laboratory observations where females failed to oviposit even when placed directly onto these galls. In these trials, small galls were still significantly less susceptible to parasitism than were medium-sized galls. A second possibility is that females oviposit in small galls less often because the hosts they contain are less suitable. In many hymenopterous parasitoids, male eggs are laid on smaller, poorer quality hosts since male reproductive fitness is less tightly linked to body size (Charnov *et al*. 1981, Godfray 1994). If this is true for *R. strobiloides* and *T. cecidomyiae,* then galls containing male parasitoids should be smaller than those galls containing females. In a sample of 265 galls for which the sex of *T. cecidomyiae* pupae could be determined, the average diameter of galls containing males ($\bar{x} = 11.06$ mm, $n = 103$) was slightly smaller than that of females ($\bar{x} = 11.56$) but not significantly so ($t = 1.32$, $P = 0.19$, $\alpha = 0.05$, $\beta = 0.2$, minimum detectable difference = 1.0 mm). The third, and perhaps most likely explanation is that *T. cecidomyiae* avoids attacking small galls because of the increased risk of subsequent predation by birds. Over the range of gall sizes for which *T. cecidomyiae* and bird attacks overlap (3-15 mm, Fig. 2-4), there is a substantial increase in the bird predation rate with decreasing gall size (Fig. 2-4, third row, dashed line).

The size-dependent patterns of attack by birds are characterised by a preference for small galls generally, with a slight shift in preference toward larger galls in 1998 and 1999 compared to 1996 and 1997. The impact of this shift is magnified by the large proportion of galls in the 10-15 mm size range. These results suggest birds are foraging for galls such that they are maximising the profitability of their attacks (*sensu* Royama 1970). If the cost associated with pecking through more gall tissue increases faster than does the potential benefit of getting a larger insect, the most profitable choice is to attack the smallest galls, which is what I observed in all years (Fig. 2-4). Galls collected in the winter of 1997 were a mixture of the 1997 cohort that contained insects and older cohorts (1996 and earlier) that were empty. If birds could not distinguish new galls from old then approximately one quarter of attacks in that winter were on empty galls thus decreasing the average benefit. In 1998 and 1999 (the post-removal years), all of the galls available to birds were new and virtually all contained insects. This increase in the average benefit made larger galls more consistently profitable warranting the extra cost of attack. Thus, the shift in size preference, particularly between 1997 and 1998, is probably associated with an increase in the average benefit between years.

The interaction among mortality factors, which are largely governed by the size-dependent patterns of attack, may have interesting dynamical consequences. In my study, the removal of galls in 1997 was a significant perturbation to an otherwise stable community. This allowed us some insight into how this community might respond to natural changes in gall density. In the first year following the removal I saw complete recovery of the midge population to pre-removal density (Fig. 2-1) indicating substantial colonisation ability in this species at this spatial scale (30 ha). With an increase in the proportion of new galls in 1998, bird foraging efficiency, and the total predation rate, increased. This relationship between foraging efficiency and the proportion of new galls in the habitat would also have a regulatory effect on natural fluctuations in gall densities. The magnitude of this regulatory effect however, may be offset by the increased overlap in gall preference between birds and *T. cecidomyiae* in the moderate gall sizes. This increased overlap explains, in part, why I saw a three-fold decrease in density of *T. cecidomyiae* in the generation after the removal. The decreased attack rates (Fig. 2-4) and the spatial distribution of attacks (Chapters 3 and 4) show that *T. cecidomyiae* disperse weakly from neighbouring populations which contributes to these lower densities. Reduced competition between *Gastrancistrus* and *T. cecidomyiae* and the better colonisation abilities of *Gastrancistrus* (Chapter 4) also explains the three-fold increase in abundance of *Gastrancistrus* one and even two generations after the removal.

Despite some differences in details among years, the interaction of the four mortality factors results in a consistent size-dependent pattern of survival for midges while in the gall (Fig. 2-1). In all years, survival increases from less than 20% in the smallest size classes to 60-90% in the largest galls. The maximum rate of increase in survival with increasing gall size occurs in galls 13.5 mm in diameter. This pattern of survival produces intense selection for larger gall size, and if gall size is a heritable trait in *R. strobiloides*, as has been found in other galling Diptera (Weis & Abrahamson 1986), it will promote the evolution of larger gall diameters. Although somewhat circumstantial, this pattern of selection supports the hypothesis that galls have evolved as a defence against parasitism and predation (Price *et al.* 1987).

In summary, gall size in *R. strobiloides* is a powerful predictor of both the type and magnitude of natural-enemy induced mortality. I have shown that from the perspective of a natural enemy, not all galls are created equally. The susceptibility of a gall to attack, and its ultimate fate, is highly dependent on its diameter, conditioned by the type of natural mortality to which it is exposed. Furthermore, patterns of attack seem to be shaped by interactions among natural enemies. This information is a valuable step toward understanding the mechanisms generating patch-level heterogeneity of risk. In Chapter 3, I will use this information to generate patch quality estimates that are specific to each parasitoid species. This is useful for accurately estimating the dispersal patterns of the parasitoids based on the distribution of their progeny. In Chapter 4, I will examine how variation in gall size directly affects the coexistence of the two parasitoid species, and the dynamics of the host-parasitoid community in general.

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47

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Table 2-2: Analysis of variance in gall diameter explained by willow clones.

Year	Source of Variation	d.f.	Mean Square	Percent of Variation	P
1996	Among willows	167	37.03	37.28	< 0.001
	Within willows	599	10.49		
1997	Among willows	243	64.78	32.47	<0.001
	Within willows	2093	12.23		
1998	Among willows	245	56.84	32.77	<0.001
	Within willows	1771	11.73		
1999	Among willows	303	87.40	29.57	<0.001
	Within willows	3191	16.74		

Table 2-3: Temporal correlation in gall diameter.

Years	n	r	P
1996-97	148	0.312	< 0.001
1997-98	172	0.301	< 0.001
1998-99	204	0.319	< 0.001
1997, 1999	198	0.217	0.002
1996, 1998	132	0.273	0.002
1996, 1999	145	0.214	0.010

Figure 2-1. Distribution of gall diameters (top row) in the total population each year and over-all survival functions (bottom row) for *R. strobiloides* in each sample year as a function of gall size. Large points represent the proportion of midges surviving in each 1.0 mm gall size class. The small points are the fitted values and corresponding standard errors based on a cubic-spline function fit to the original binomial data (not the group means) with approximately 4 degrees of freedom.

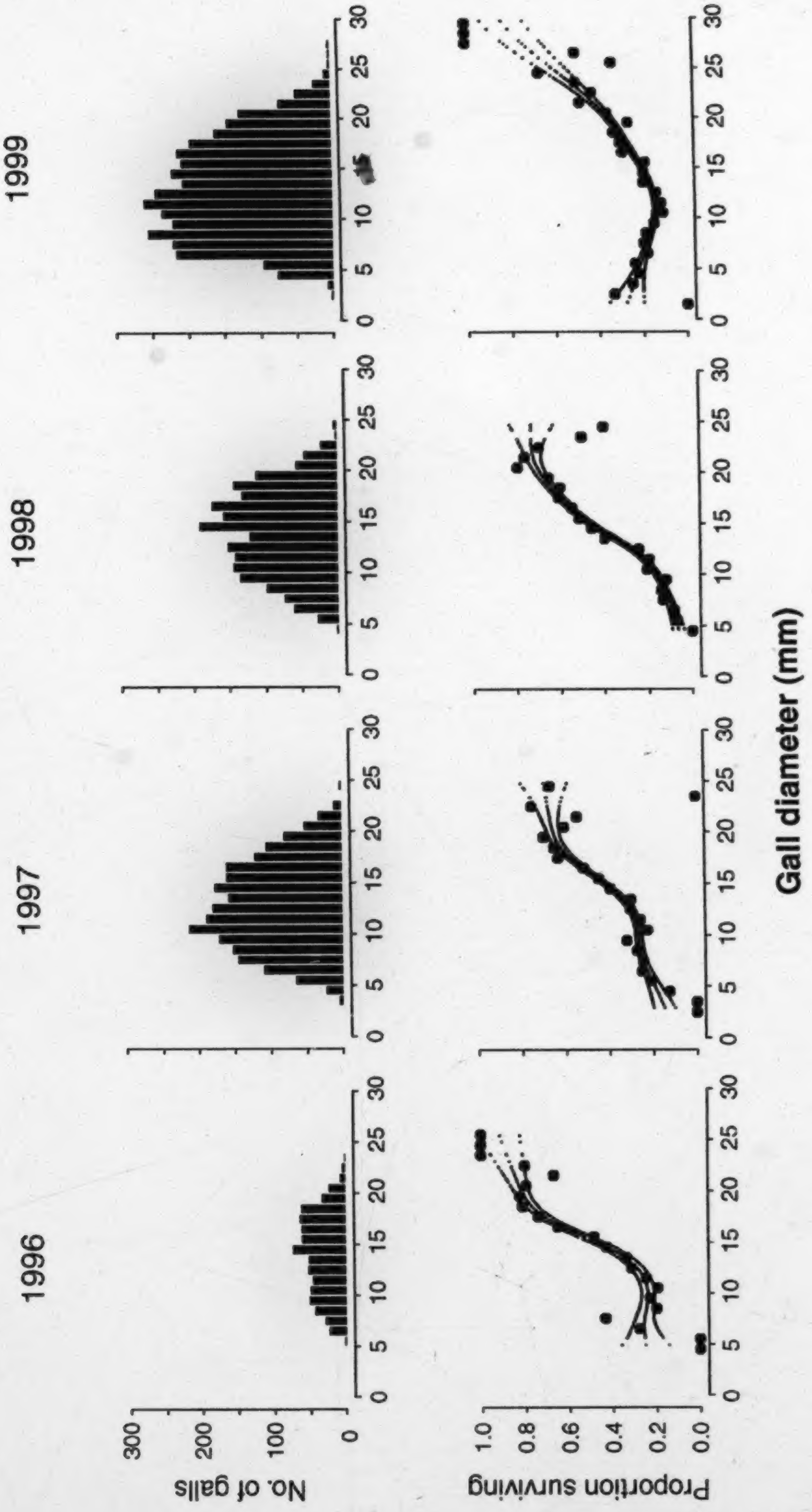

1996
1997
1998
1999
No. of galls
300
200
100
0
Proportion surviving
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
Gall diameter (mm)

Figure 2-2. Observed mortality rates in *R. strobiloides* for each sample year (columns) and each mortality factor (rows) as a function of gall size. Large points represent the proportion of galls in each 1.0 mm size attributed to each mortality factor. Small points are calculated as in figure 1b. Vertical dashed line represents the average gall diameter over all years as a reference. Bird predation in 1999 multiplied by 10 for clarity.

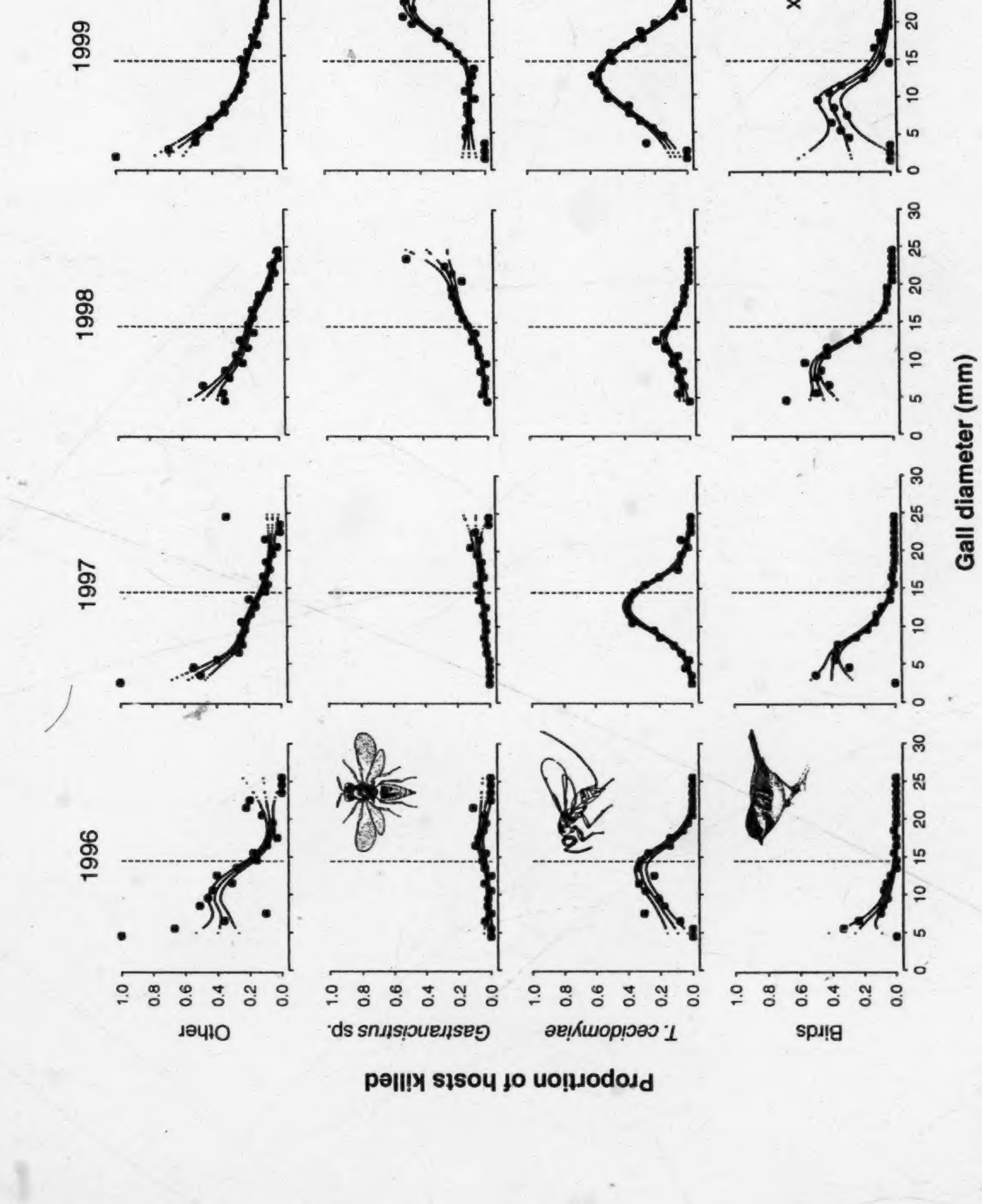

1996
1997
1998
1999
Other
Gastrancistrus sp.
T. cecidomyiae
Birds
Proportion of hosts killed
0.0
0.2
0.4
0.6
0.8
1.0
x 10
0
5
10
15
20
25
30
Gall diameter (mm)

Figure 2-3. Observed proportion of *R. strobiloides* galls multiparasitised vs. the expected proportion if the parasitoids *Gastrancistrus* and *Torymus* had attacked galls independently. Each point represents the proportion of galls in 1.0 mm diameter classes that were parasitised by both species. Predicted proportions are calculated from the product of the observed marginal rates of attack for each species under the assumption of random overlap in host use. The diagonal line is the expected 1:1 relationship indicating random association.

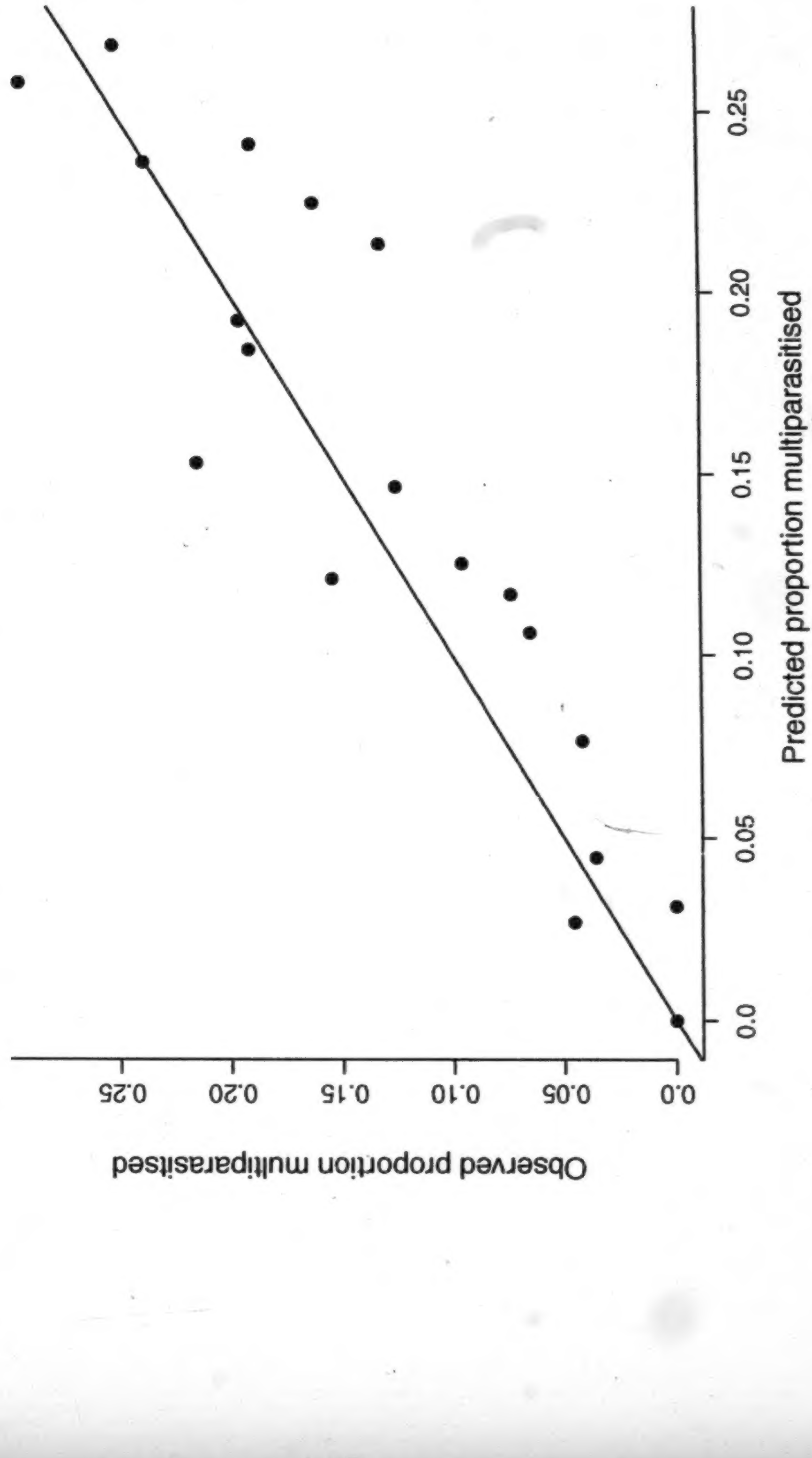
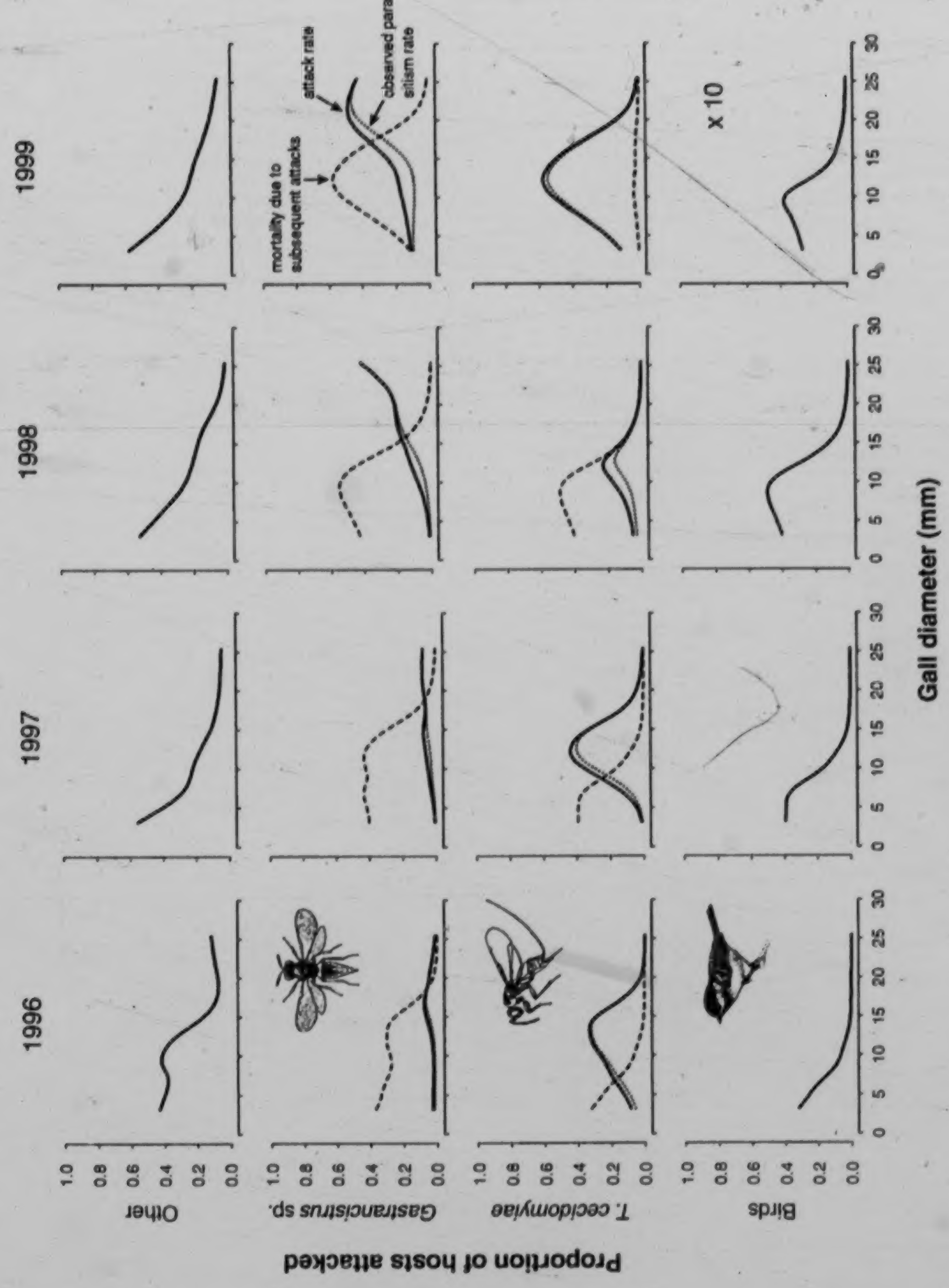

Observed proportion multiparasitised
0.0
0.05
0.10
0.15
0.20
0.25
Predicted proportion multiparasitised
0.0
0.05
0.10
0.15
0.20
0.25

Figure 2-4. Estimated attack rates for each year (columns) and mortality factor (rows). Size-dependent marginal attack rates (solid line) were calculated from the observed parasitism rates (dotted line) by accounting for the proportion of attacks that were masked by subsequent mortality factors (dashed lines). Dotted lines are identical to the observed rates of parasitism in Figure 2-2. Bird attacks in 1999 multiplied by 10 for clarity.


1996
1997
1998
1999
Proportion of hosts attacked
Other
Gastrancistrus sp.
T. cecidomyiae
Birds
1.0
0.8
0.6
0.4
0.2
0.0
Gall diameter (mm)
0
5
10
15
20
25
30
mortality due to subsequent attacks
attack rate
observed parasitism rate
x 10

Chapter 3:
Differential dispersal rates predict chaos in a natural host-parasitoid community

INTRODUCTION

Recently, there has been considerable theoretical interest in the effects of differential dispersal rates in stabilising host-parasitoid models (Reeve 1988, Hassell, Comins & May 1991, Comins, Hassell & May 1992, Comins & Hassell 1996, Rohani, May & Hassell 1996). Although the specific predictions of each of these models are difficult to compare due to differences in model formulation, the results of these studies generally suggest that the relative dispersal rates of the host and its specialist parasitoids could be an important factor governing the global stability of host-parasitoid communities in spatially subdivided habitats and populations.

Several studies have attempted to measure the dispersal rates in host-parasitoid communities directly (Hopper 1984, Cappuccino 1992, Dempster et al. 1995, Jones Godfray & Hassell 1996, Lei & Hanski 1998), indirectly [Lei & Hanski 1998, Maron and Harrison 1991, van Nouhuys & Hanski (in press)] or experimentally by studying the effects of dispersal on population dynamics (Briggs & Latto 2000). However, the results of field studies are often difficult to interpret within the framework of existing theoretical literature. Techniques such as mark-release-recapture or mass-marking may have undesirable effects on the behaviour of the individuals, thus introducing unknown biases in movements (Turchin 1998). Similarly, estimating dispersal by studying the colonisation of empty habitat may not be a useful alternative when the majority of dispersal events occur in occupied habitat. Although manipulative experiments can be powerful for testing hypotheses with respect to the effect of dispersal on dynamics, they are generally unsuitable for parameterising dispersal models.

In this paper, I estimate the dispersal of a single host species and its two specialist parasitoid species in a natural network of habitat patches using population census data only. In general, I do this by 1) measuring population sizes in each patch at a given point in time, 2) measuring population sizes in the same patches one generation later after both dispersal and reproduction, and 3) modelling the changes in these population sizes as a function of dispersal between patches and growth within patches. By using a defined dispersal-growth model (which may vary among the three species) I can simulate the spatio-temporal dynamics of these populations to determine if differential dispersal rates help stabilise the host-parasitoid interactions in this community within the context of existing theory.

METHODS

Description of the host-parasitoid-parasitoid community

Rabdophaga strobiloides (Cecidomyiidae) is a univoltine and solitary bud-galling midge with a transcontinental distribution in North America (Gagné 1989). Wilson (1968) provides an account of the life cycle in Michigan where the midge forms galls predominantly on the heart-leafed willow, *Salix eriocephela* Michx. At my study site in Alberta, Canada, the only notable difference in the biology of this insect is that it forms galls predominantly on Bebb's willow, *S. bebbiana* Sarg.

Adult midges emerge synchronously from galls in mid to late May. Females are mated within hours of emergence and lay eggs singly on the lower surface of leaves on expanding terminal shoots. Egg hatch occurs within 2-3 days, after which the first instar larva crawls to the apical meristem and begins feeding. Gall diameter increases throughout the summer (June – September) in a sigmoidal pattern (Weis & Kapelinski 1984) during which time the larvae pass through three instars. At my study site, galls reach their maximum size by September and range from 2.8 mm to 29.7 mm in diameter (mean = 13.84, n = 7184). Pupation occurs within the gall the following spring. After midges emerge, galls remain on the willows for up to four years.

In Alberta, *R. strobiloides* larvae are commonly attacked by two species of parasitoids. Adult female *Gastrancistrus* sp. (Hymenoptera: Pteromalidae) emerge from the previous generation of galls in June and attack new galls containing first instar midge larvae. These solitary koinobionts oviposit through the gall tissue and lay a single egg within the host larva. Galls are also parasitised by *Torymus cecidomyiae* (Walker) (=*strobiloides*) (Hymenoptera: Torymidae). These solitary idiobionts emerge from the previous year's galls in early August and attack the current year's galls when they have nearly reached their final size. The female parasitoids use their long ovipositor to deposit a single egg on the midge larva or in the larval chamber. Both parasitoid species remain within the gall during their larval and pupal stages. Although it is difficult to be certain that these parasitoids are strict specialists on *R. strobiloides*, there is no record in the literature of there being other hosts, nor have they been found in collections of other species of galls in the study area (B. Van Hezewijk, personal observation).

Description of the study site and census techniques

The study was conducted in a 20 ha area of the Rumsey Ecological Reserve (Fig. 3-1), Alberta, Canada (51°55'N, 112°38W). The reserve is situated on the southern limit of the aspen parkland ecoregion (Strong & Leggat 1992). When combined with the Rumsey Natural Area to the south, it comprises the largest area of undisturbed aspen parkland left in Canada (Fehr 1982). The topography is characterised as 'knob and kettle' or hummocky where the landscape is dominated by a regular arrangement of wet depressions. The vegetative community is primarily fescue prairie grassland dominated by *Festuca hallii* (Vasey) Piper, *Stipa* spp. and *Agropyron* spp., with patches of *Populus tremuloides* Michx., *Salix* spp. and *Rosa* spp. (Strong & Leggat 1992). The most common species of willows are *Salix petiolaris* J.E. Smith and *S. bebbianna*, but galls have never been found on the former species at my study site.

In April 1999, the entire study area was surveyed for galls formed in 1998. Each willow on which galls were found was mapped on 1:5000 aerial photographs and assigned a unique number with a metal tag. The number of galls on each willow, and the proportion that had been previously attacked by birds was recorded, but galls were left *in situ* to allow normal emergence of midges and parasitoids. In December 1999, each willow was revisited and all of the 1998 and the new 1999 galls were collected.

In the laboratory, the minimum diameter of each gall at its widest point was measured to the nearest millimetre using callipers. The fate of each gall, whether it produced an adult *R. strobiloides*, *Gastrancistrus*, or *Torymus,* was determined by dissection. For the 1998 cohort of galls, the majority of which did not contain insects, gall fate was determined using characters of the vacant gall that were reliably associated with each gall fate (Appendix A).

The 1:5000 scale aerial photographs were scanned as a 256-grayscale image with a resolution of 375 pixels / 2.54 cm. The centre of each gall-bearing willow was represented in this image by a single black pixel. The relative location of each willow, represented by a pair of x,y-coordinates, were then extracted from the image with an approximate precision of 0.34 m.

Dispersal among patches

Without *a priori* knowledge of the distribution of dispersal distances for each of the three species in this community I adopted a flexible strategy based on four commonly used dispersal functions. In general, it is reasonable to assume that the probability of moving from a natal patch *i* to another patch *j* decreases with increasing distance *d.* Both the exponential and power functions can describe this pattern and have been used with differing degrees of success to model empirical data for insect dispersal (Turchin & Thoeny 1993, Nieminen 1996, Lele, Taper & Gage 1998, Roslin 2000). To make these functions more relevant to the *Rabdophaga* community I included a parameter μ, describing the proportion of individuals that dispersed from their natal patch. Thus, for the exponential model the proportion of individuals in patch *i* which emigrated to patch *j* can be expressed as:

$$k_{ij} = \delta^{d_{ij}} \qquad \text{eqn 1}$$

subject to the constraint that the sum of k_{ij} over all patches, where $j \neq i$, is equal to the proportion μ of the population in each patch which emigrated. For the power function, the proportion of individuals in patch *i* which emigrated to patch *j* is:

$$k_{ij} = d_{ij}^{\ -\delta} \qquad \text{eqn 2}$$

where the same summation constraint is applied so that the total proportion of individuals leaving a patch is μ. I also used the more common formulation in which the rate of emigration is not a fixed proportion. In this case the proportion of individuals in patch *i* which emigrated to patch *j* is given by:

$$k_{ij} = b\, d_{ij}^{\ -\delta} \qquad \text{eqn 3}$$

where *b* is a constant related to the intensity of the source patches. In this case the proportion of individuals that emigrated from a patch depends on the number and proximity of neighbouring patches. Lastly, I modelled dispersal following the methods of Hassell, Comins & May (1991) where a fixed proportion, μ, of individuals in a patch migrated to the eight nearest neighbouring patches. The proportion of individuals in patch i which emigrated to patch j is simply:

$$k_{ij} = \mu / 8 \qquad \text{eqn 4}$$

where j runs over the eight nearest neighbours of patch i.

For all the models, the number of adult individuals X, of species s, in patch i, and time t, following dispersal is then:

$$X'_{s,i,t} = X_{s,i,t} - \sum_{j \neq i} k_{i,j} X_{s,i,t} + \sum_{j \neq i} k_{j,i} X_{s,j,t} \,. \qquad \text{eqn 5}$$

Within-patch processes

The within-patch dynamics of this community is described by three important facts. First, *Torymus* attacks hosts later in the season than does *Gastrancistrus*, and in all cases, wins larval competition in multiply parasitised hosts (Chapter 2). Second, the probability of successful attack by each parasitoid species is highly dependent on gall diameter (Chapter 2). Third, average gall diameters differ significantly among patches (range = 3.4, 23.8mm). To incorporate these facts into a population model, I started with Hassell's (1978) formulation for a host-parasitoid-facultative hyperparasitoid community given by:

$$\begin{aligned} N_{t+1} &= \lambda\, N_t\; f_1(P_t)\, f_2(Q_t) \\ P_{t+1} &= \lambda\, N_t\; f_2(Q_t)\, [1-f_1(P_t)] && \text{eqn 6} \\ Q_{t+1} &= \lambda\, N_t\; [1-f_2(Q_t)] \end{aligned}$$

where $f_1(P_t) = e^{-a1Pt}$, $f_2(Q_t) = e^{-a2Qt}$, and N, P and Q are the numbers of adult *Rabdophaga*, *Gastrancistrus*, and *Torymus* respectively.

The effect of gall size was included in the model by assuming that differences in the average susceptibility of galls, due to differences in average gall diameter, translated into proportional refuges from parasitism. I believe this was reasonable since it was previously found that although the total parasitism rate changed substantially between years, the shape of the functions relating rates of parasitism to gall size varied little (Chapter 2). Including parasitoid-specific refuges into equation 6 resulted in:

$$\begin{aligned} N_{t+1} = \lambda\, N_t\; \big(&f_1(P_t)\, f_2(Q_t) && c \\ &+ (1-\gamma_P)\, [1-f_1(P_t)]\, f_2(Q_t) && b \\ &+ (1-\gamma_Q)\, [1-f_2(Q_t)]\, f_1(P_t) && f \\ &+ (1-\gamma_P)\, [1-f_1(P_t)]\, (1-\gamma_Q)\, [1-f_2(Q_t)]\; \big) && e \qquad \text{eqn 7} \\ P_{t+1} = \lambda\, N_t\; \big(&\gamma_P\, [1-f_1(P_t)]\, f_2(Q_t) && a \\ &+ \gamma_P\, [1-f_1(P_t)]\, (1-\gamma_Q)\, [1-f_2(Q_t)]\, \big) && d \\ Q_{t+1} = \lambda\, N_t\; \big(&\gamma_Q\, [1-f_2(Q_t)]\, \big) && g,h,i \end{aligned}$$

where γ_P and γ_Q are the proportion of hosts susceptible to parasitism by *Gastrancistrus* and *Torymus* respectively and f_1 and f_2 are as in equation 6. The letters following each line correspond to an area in the geometric representation of this system of equations (Fig. 3-2).

To define the proportion of susceptible hosts in each patch I used empirically derived non-linear relationships between the frequency of parasitoid attack and gall diameter for each of the two parasitoid species (Chapter 2). The original functions were derived from rates of parasitism in a nearby study site using the 1999 cohort of galls (Fig. 3-3). These functions were then scaled such that the maximum observed attack rate corresponded to 100% susceptibility. This assumes that the maximum level of parasitism was not achieved for reasons other than gall suitability.

The dispersal-growth model

In combining these two processes I assume that dispersal occurs first, followed by local reproduction and parasitism. The post-dispersal adult populations $N'_{i,t}$, $P'_{i,t}$, and $Q'_{i,t}$ are calculated using equation 5. These quantities are then substituted for $N_{i,t}$, $P_{i,t}$, and $Q_{i,t}$ in equation 7 to generate the population sizes in the next generation.

Model fitting and selection

The data to which this model was applied consisted of 1) the numbers of *R. strobiloides* ($N_{i,t}$), *Gastrancistrus* ($P_{i,t}$), and *Torymus* ($Q_{i,t}$) emerging from 1998 galls on each of 232 willows, 2) the numbers of each species, on each willow, after dispersal and reproduction ($N_{i,t+1}$, $P_{i,t+1}$, $Q_{i,t+1}$), 3) the average susceptibility of 1999 galls on each willow, and 4) the location of each willow.

To simplify the estimation procedure in a model with many parameters I divided the problem into three parts. First, I assume that the numbers of established galls produced in 1999 is directly proportional to the number of *Rabdophaga* eggs laid on a willow. If this assumption is valid then one can infer that the distribution of galls is an accurate reflection of the dispersal of female midges and the distribution of their progeny. This also allows one to estimate the dispersal of the midge independent of any subsequent parasitoid mortality because parasitoid attack does not prevent the formation of galls. Next, I estimated the parameters for the *Torymus* sub-model (Q) because its attacks on galls are independent of prior parasitism by *Gastrancistrus* (P) (Chapter 2). For this sub-model I use observed 1999 gall numbers in place of $\lambda N'_t$. Lastly, I fit the sub-model for *Gastrancistrus* (P) using the observed 1999 gall numbers in place of $\lambda N'_t$ and the previously estimated parameters associated with the attack (a_2) and dispersal (δ,μ) of *Torymus*. In all cases, the best fitting parameters were found by minimising the sum of squared deviations between the observed population numbers and those predicted by the model using the bounded non-linear minimisation procedure NLMINB in S-Plus 2000 (MathSoft 1999).

For each species, four alternative reduced models were fit to the data in addition to the four dispersal models described above. Model 1 (Table 1), in which both δ and μ are set to zero, corresponds to no dispersal. Model 2, with $\delta = 1$, corresponds to global dispersal of a proportion μ of all individuals. This type of model has been extensively studied by Nachman (1987 a,b), Reeve (1988), and Taylor (1988). In model 3, all individuals emigrate from their natal patches ($\mu = 1$) but disperse to neighbouring patches according to the exponential function. Finally, in model 4, both δ and μ are set to one, such that all individuals enter a pool of dispersers which move equally to all other patches (Hassell & May 1973, 1974, Hassell, Comins & May 1991).

Approximate confidence limits on the estimated parameter for all models were obtained using a cross-validation procedure based on the bootstrap method (Efron & Tibshirani 1993). To maintain the necessary spatial information in the data, sub-samples were not completely random but consisted of all the willows within spatially contiguous sub-sections of the study area. The circular sub-sections had diameters of 200 m with centres randomly located within the region depicted in figure 3-4. For each of 1000 randomly located sub-sections, model parameters were estimated using the previously outlined procedure. Approximate 95% confidence limits for each parameter were then estimated from the 2.5 and 97.5 percentiles of the resampled distributions.

The best fitting model was selected based on the criterion proposed by Efron & Tibshirani (1993) in which the residual sum of squares for a model with m parameters is adjusted using the relationship: $SS_{adj} = SSQ_m / (n - 2m)$, where n is the number of data points.

RESULTS

Spatial and temporal patterns in abundance

Among the 232 willows in the study area, gall numbers were generally low (median number of galls/willow = 2.0 and 3.0 for 1998 and 1999) but extremely variable (ranges = 0-211, 0-168). Between 1998 and 1999 there was a significant positive correlation in the numbers of *Rabdophaga*, *Gastrancistrus*, and *Torymus* within willows (Spearman's Rank Correlation (SRC) = 0.286, $P < 0.001$; 0.363, $P < 0.001$; 0.325, $P < 0.001$ respectively).

In 1998, there was a weak positive correlation between the number of *Rabdophaga* on a willow and the number of *Rabdophaga* on the nearest neighbouring willow (SRC = 0.141, $P = 0.032$) but this association was non-significant in 1999 (SRC = 0.111, $P = 0.091$). Similarly, the numbers of *Gastrancistrus* on neighbouring willows were weakly correlated in 1998 (SRC = 0.144, $P = 0.023$) but not in 1999 (SRC = 0.088, $P = 0.173$). Numbers of *Torymus* were not correlated among willows in either 1998 or 1999 (SRC = 0.012, $P = 0.852$; SRC = 0.078, $P = 0.238$).

Changes in the number of galls between the two years were highly variable among willows (Fig. 3-5) and were uncorrelated between nearest-neighbours (SRC = 0.035, $P = 0.595$). Changes in the numbers of *Gastrancistrus* and *Torymus* were also quite variable and were similarly uncorrelated between nearest-neighbours (SRC = 0.128, $P = 0.052$; SRC = 0.059, $P = 0.454$).

Host dispersal

I found the abundance and spatial arrangement of midges (galls) among willows in 1999 was best explained by the three parameter model incorporating local population growth, a uniform emigration rate, and dispersal described by the power function (model 6, Table 2). The data supported this model only marginally better than exponential dispersal with the same number of parameters (model 5) but substantially better than either global dispersal of all individuals (model 4) or local dispersal of all individuals (model 3). The power function model predicted highly localised dispersal with only 24% of individuals dispersing from the natal willows and most of those individuals dispersed to willows within 40m (Fig. 3-6a). Overall, predictions were consistent with the observed data (Fig. 3-7a) except in willows with no galls in 1999 where the model produced systematic overestimates.

Parasitoid dispersal

In general, both parasitoid species dispersed far more widely than did the host species in this community. For *Gastrancistrus*, every model that incorporated some form of dispersal (models 2-7) predicted global dispersal of all individuals, and as such, all fit equally well (Table 3). Random searching and global dispersal did, however, accurately predict the observed numbers of *Gastrancistrus* for most willows (Fig. 3-7b). Again, the model overestimated the abundance of parasitoids in willows where none were observed. This is not a carry over effect from the same failure in the

Rabdophaga model because the actual rather than the predicted host distribution in 1999 was used in the estimation of the 1999 parasitoid abundances.

For *Torymus*, the model that best explained the observed pattern of parasitism among willows incorporated random search within willows, a uniform emigration rate, and exponentially decreasing dispersal between willows (model 5, Table 4). This model predicted 97.5% emigration of individuals from the natal patch, with 50% of emigrants dispersing more than 100m (Fig. 3-6b). The reduced model with exponential dispersal, but emigration fixed at 100% (model 3) performed nearly as well but was not substantially different from the best fitting model. The other models produced significantly worse fits to the data. For most willows, the exponential dispersal model accurately predicted the observed abundance of *Torymus* (Fig. 3-7c) with the exception of willows in which no *Torymus* were observed.

DISCUSSION

I found that only 25% of hosts emigrated from their natal patch, and of those emigrants, dispersal was generally limited to less than 40m and was best described by a power function. In contrast, the two parasitoid species had very high emigration rates (97.5 - 100%) and dispersed widely throughout the study area. Using the model-fitting approach to estimating these dispersal rates allowed these results to be placed in the context of existing theoretical models. Following the methods of Hassell, Comins & May (1991) I used my estimated dispersal and population growth parameters to perform numerical simulations of the host-parasitoid interactions on a 30x30 lattice of habitat patches. For ease of comparison with their results I assume in these simulations that each patch is identical inasmuch as gall diameter has no effect on parasitism rates.

Nearest-neighbour dispersal (model 8), which is most commonly used in theoretical models, produced chaotic spatio-temporal patterns in which *Rabdophaga* and *Torymus* persisted but *Gastrancistrus* quickly became extinct (Fig. 3-8a). This is consistent with the results of a similar model explored by Comins & Hassell (1996) where the competitively inferior parasitoid (in their case, the species with the lower searching efficiency) was unable to persist unless it possessed dispersal rates an order of magnitude higher than that of the superior competitor. In my case, the two parasitoids were estimated to have similar dispersal abilities and searching efficiencies (Tables 3, 4). *Gastrancistrus*, however, is considered the inferior competitor because it is assumed in the model (and supported by data; Chapter 2) that its larvae are always killed by *Torymus* in multiply parasitised hosts.

When I used the best-fitting models for each species in the simulations, all runs resulted in the extinction of all three species in less than 10 generations under a variety of starting conditions (Fig. 3-8b). This seems to be mainly due to the high dispersal ability and competitive dominance of *Torymus* allowing it to colonise all the patches in the network. This effectively reduces the spatial extent of the habitat, thus promoting the highly unstable host-parasitoid dynamics more typical of non-spatial population models with very efficient parasitoids (Hassell 1978).

Clearly, neither of the previous simulations is a very good representation of field populations that seem to be characterised by low spatial synchrony, regional coexistence of both parasitoid species, and densities and parasitism rates that, over the ensemble of willows, are remarkably constant through time (B. Van Hezewijk, unpublished data). These results seem to show that even biologically realistic spatial models fail to add the stability required to capture the key dynamical properties of this host-parasitoid community. The obvious over-simplification in my simulations is the exclusion of any refuge effects due to differences in gall size. In Chapter 2 I found that gall size is an important factor affecting parasitism rates. In a third simulation (Fig. 3-8c) I used the best-fitting dispersal functions but also included variability in average gall diameter among willows and between years. This produced much more spatial and temporal heterogeneity in host abundance and parasitism rates but was more stable over the ensemble, resulting in host persistence and long-term coexistence of both parasitoid species.

A deficiency common to the best fitting models for each species was an overestimation of the abundance of insects on willows where none were actually observed (Fig. 3-7). This could be due to two causes. First, if the populations exhibit an Allee effect, a small number of migrants that arrive at previously vacant willows may not reproduce and therefore not be detected in my census. Because none of the models includes this effect, predictions at low densities would necessarily be too high. This explanation seems unlikely since, over most of the habitat, these species occur in very sparse numbers and are probably well adapted to successful reproduction at low densities. A more likely explanation for the discrepancy between observations and predictions is due to the particular structure and deterministic nature of dispersal in the models. For all parameter combinations producing some dispersal (except for model 8), the models predict that all willows will get at least some immigrants, and that these immigrants will go on to reproduce. In reality, many willows, especially those that are most isolated, will remain uninhabited due to the stochastic events that most strongly affect low-density populations. Wilson and Hassell (1997) found in their simulations that demographic stochasticity tended to cause greater variability in space and time, and that it was likely the stochastic component of dispersal which made the greatest contribution to this effect. Although they found that this tended to destabilise the dynamics, including stochasticity in my models would produce more asynchronous patch dynamics and thus mimic observed population trajectories more closely.

Dispersal rates of a host insect and its associated parasitoids were estimated by explicitly modelling the effect that between-patch migrations have on local population numbers. Under the parameter values estimated from the data, nearest-neighbour dispersal did not allow the coexistence of both parasitoid species and did not produce realistic dynamics at the ensemble level. Likewise, the best-fitting dispersal functions alone did not produce realistic dynamics. However, incorporating gall-size dependent refuges into the simulation produced the added heterogeneity necessary to stabilise the ensemble dynamics enough to allow for the regional persistence of both parasitoid species. Contrary to theory, dispersal does not stabilise host-parasitoid dynamics in this community and other mechanisms are required for persistence.

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Table 3-1: Growth-dispersal models and their corresponding fixed and free parameters for each species in the host-parasitoid community. In models 2 and 4, the negative exponential model was used with $\delta = 1$ to model global dispersal of individuals among the patches.

		Parameters (N)		Parameters (P)		Parameters (Q)	
Model	Description	Free	Fixed	Free	Fixed	Free	Fixed
1	No dispersal	λ	$\delta = 0, \mu = 0$	$a1$	$\delta = 0, \mu = 0$	$a2$	$\delta = 0, \mu = 0$
2	Variable emigration, global dispersal	λ, μ	$\delta = 1$	$a1, \mu$	$\delta = 1$	$a2, \mu$	$\delta = 1$
3	Total emigration, exponential dispersal	λ, δ	$\mu = 1$	$a1, \delta$	$\mu = 1$	$a2, \delta$	$\mu = 1$
4	Global dispersal	λ	$\delta = 1, \mu = 1$	$a1$	$\delta = 1, \mu = 1$	$a2$	$\delta = 1, \mu = 1$
5	Constrained negative Exponential dispersal	$\lambda, \delta\ \mu$		$a1, \delta\ \mu$		$a2, \delta\ \mu$	
6	Constrained power Function dispersal	$\lambda, \delta\ \mu$		$a1, \delta\ \mu$		$a2, \delta\ \mu$	
7	Unconstrained power Function dispersal	$\lambda, \delta\ b$		$a1, \delta\ b$		$a2, \delta\ b$	
8	Nearest-neighbours dispersal	λ, μ		$a1, \mu$		$a2, \mu$	

Table 3-2: Parameter estimates and 95% confidence limits (in brackets) for the eight growth-dispersal models for *Rabdophaga*. Fixed parameters are shown in bold.

	Model parameters							
Model	λ		δ		μ		SS	SSpen
1	2.679	(2.138, 3.622)	**0**		**0**		42503.64	184.80
2	3.394	(2.785, 4.757)	**1**		0.253	(0.139, 0.356)	41216.72	180.78
3	2.796	(2.323, 4.160)	0.511	(0.000, 1.000)	**1**		102059.0	447.63
4	3.341	(2.673, 4.560)	**1**		**1**		106431.1	462.74
5	3.287	(2.688, 4.677)	0.379	(0.062, 0.757)	0.245	(0.162, 0.341)	39913.3	176.61
6	3.290	(2.766, 4.760)	2.165	(0.410, 2.943)	0.239	(0.188, 0.340)	39499.5	174.78
7	3.253	(2.785, 4.757)	-1.086	(-1.616, 0.000)	0.0114*	(0.002 , 0.026)	40938.6	181.14
8	3.273		--		0.237		40563.9	177.91

* This value corresponds to the parameter *b* in the unconstrained power function and cannot be compared to the proportion of individuals emigrating.

Table 3-3: Parameter estimates and 95% confidence limits (in brackets) for the eight growth-dispersal models for *Gastrancistrus*.

Fixed parameters are shown in bold.

	Model parameters							
Model	*a1*		δ		μ		SS	Cp
1	0.028		**0**		**0**		4191.2	18.22
2	1.530		**1**		1.0		903.7	3.96
3	1.530		1.0		**1**		903.7	3.96
4	1.530		**1**		**1**		903.7	3.93
5	1.530		1.0		1.0		903.7	4.00
6	1.530	(0.798, 2.481)	0.0	(0, 0.895)	1.0	(0.992, 1.0)	903.7	4.00
7	1.561		0.0		0.0043*		902.3	4.00
8	0.939		--		0.826		3424.2	15.02

* This value corresponds to the parameter *b* in the unconstrained power function and cannot be compared to the proportion of individuals emigrating.

Table 3-4: Parameter estimates and 95% confidence limits (in brackets) for the eight growth-dispersal models for *Torymus*. Fixed parameters are shown in bold.

	Model parameters				
Model	$a2$	δ	μ	SS	Cp
1	0.560	**0**	**0**	6938.0	30.17
2	1.445	**1**	0.949	2018.8	8.85
3	1.722	0.938	**1**	1706.64	7.49
4	1.737	**1**	**1**	2291.368	9.96
5	1.551 (0.733, 2.381)	0.936 (0.722, 1.0)	0.975 (0.560, 1.0)	1594.618	7.06
6	1.508	0.409	0.961	1881.977	8.33
7	1.445	0.0	0.0041*	2018.763	8.93
8	1.230	--	0.936	4977.738	21.83

* This value corresponds to the parameter *b* in the unconstrained power function and cannot be compared to the proportion of individuals emigrating.

Figure 3-1. Aerial photograph of the study area at the Rumsey Ecological Reserve in Alberta. White dots indicate the locations of individual *Salix bebbiana*. Solid black line delineates the area censused for galls.

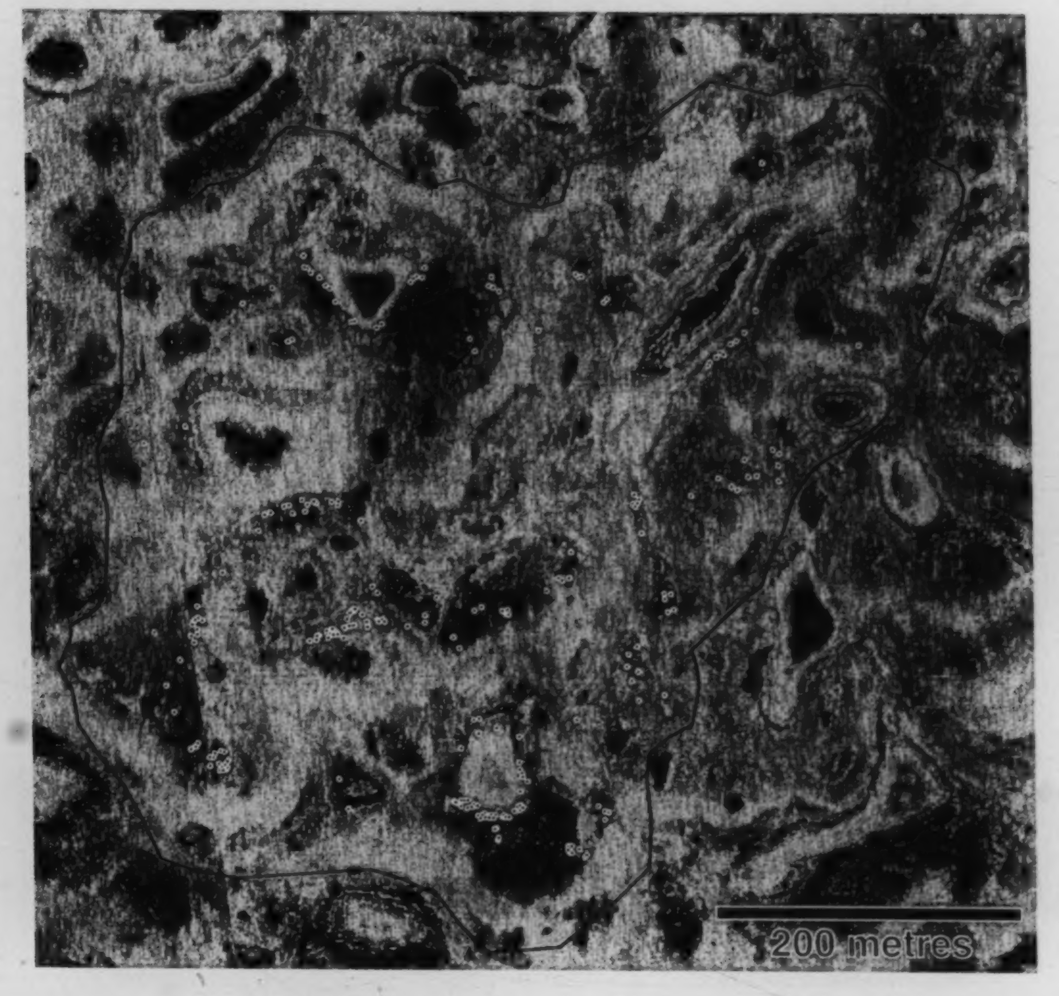

200 metres

Figure 3-2. Graphical representation of the host-parasitoid interactions defined by equation 7. The entire area of the square represents the population of hosts in generation $t+1$. Horizontal hatching indicates the proportion of hosts successfully parasitised by *Torymus* (Q). Vertical hatching indicates the proportion of hosts successfully parasitised by *Gastrancistrus* (P). White area represents the proportion of hosts that survive to reproduction. Letters in each area correspond to the quantities indicated in equation 7.

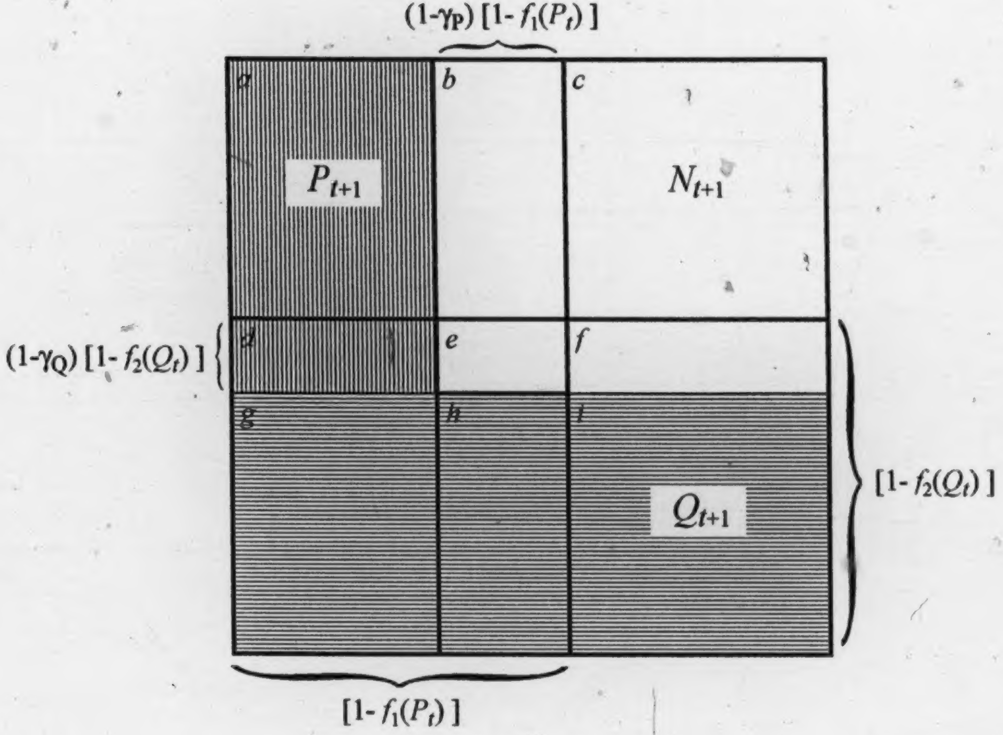

$(1-\gamma_P)\,[1-f_1(P_t)]$
a
b
c
P_{t+1}
N_{t+1}
$(1-\gamma_Q)\,[1-f_2(Q_t)]$
d
e
f
g
h
i
Q_{t+1}
$[1-f_2(Q_t)]$
$[1-f_1(P_t)]$

Figure 3-3. Size dependent susceptibility of *Rabdophaga* to parasitism by a) *Gastrancistrus* and b) *Torymus* in 1999. Large points represent the observed proportion of midges parasitised in each 1.0 mm size class from a sample of 7184 galls. The small points are the fitted values and corresponding standard errors based on a cubic-spline function fit to the original binomial data. The solid line is based on the estimated attack rate for each parasitoid species scaled such that the maximum attack rate is one (see Chapter 2 for details).

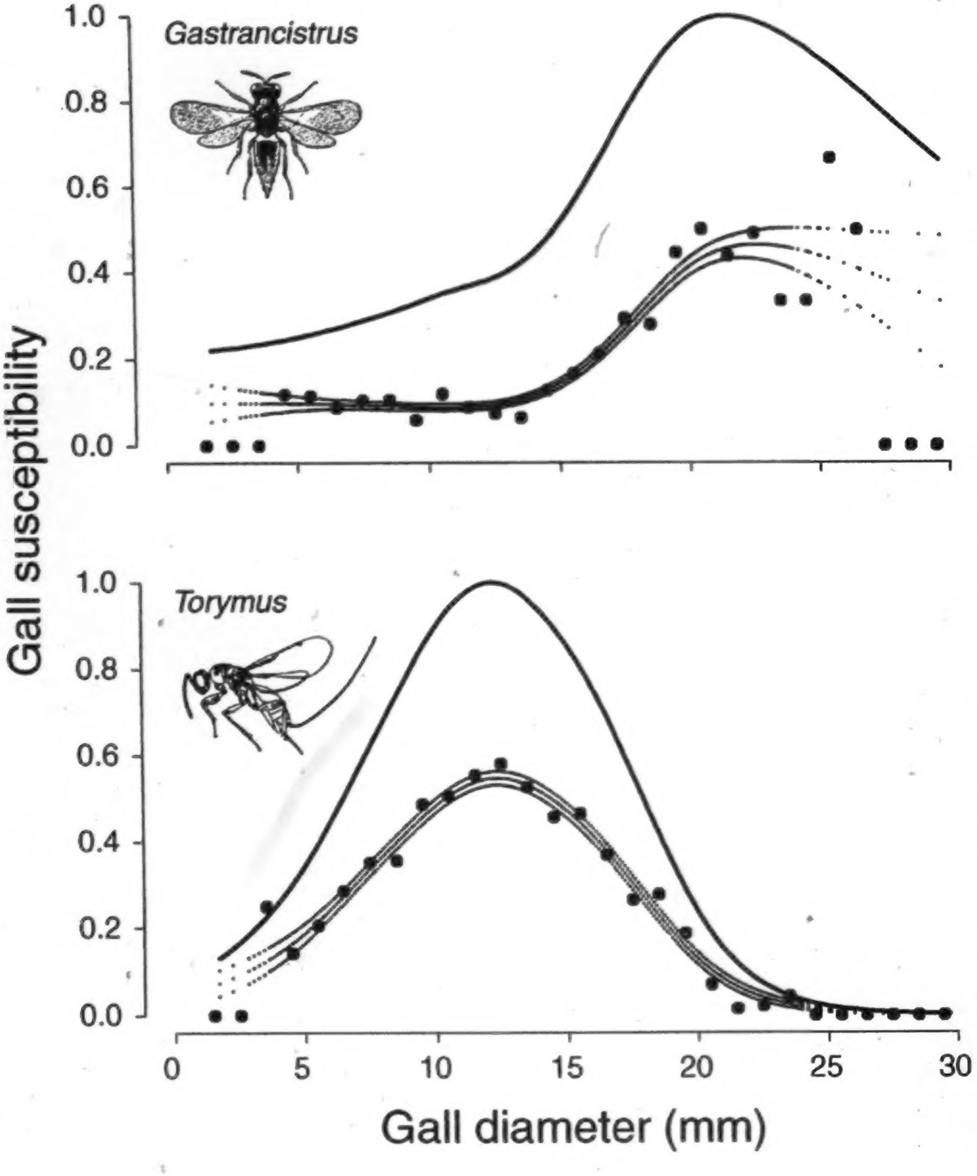

Gastrancistrus
Torymus
Gall susceptibility
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
Gall diameter (mm)

Figure 3-4. Sub-sampling scheme used to estimate confidence limits associated with model parameters. Points indicate the location of individual willows in the study area. The large circle delineates the area over which random sub-samples can be centred. Small circles represent six randomly located sub-samples.

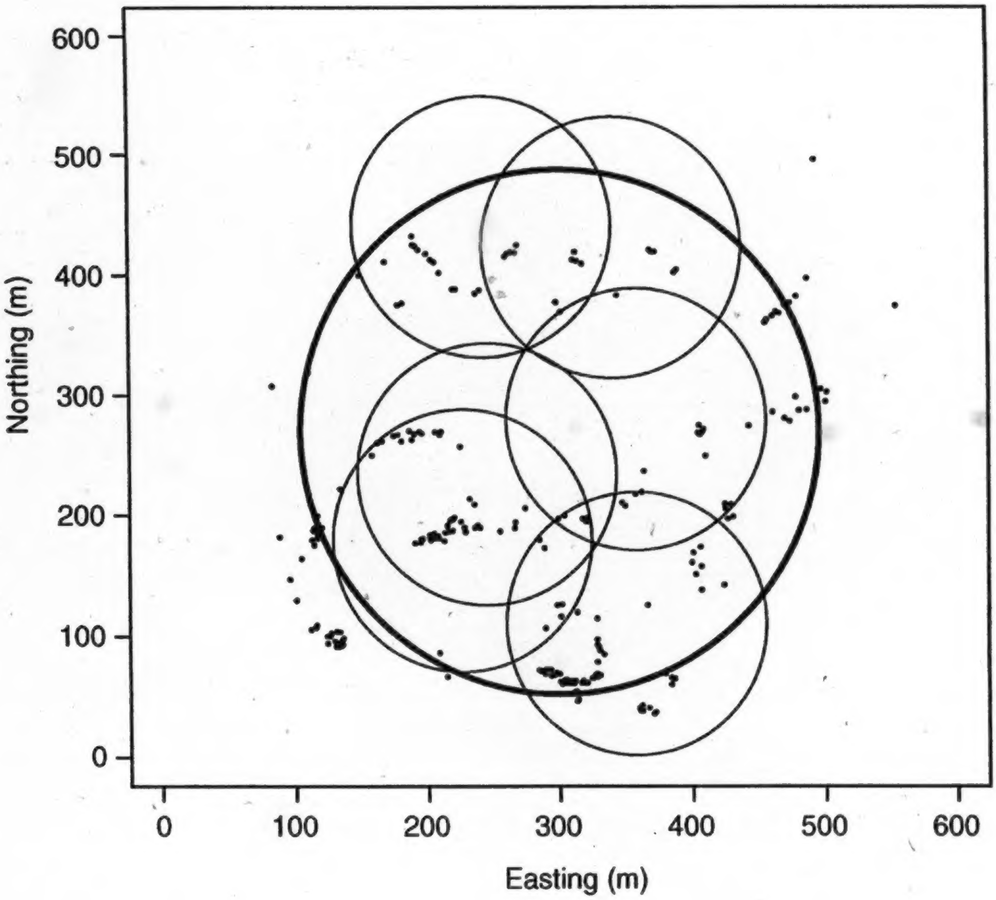
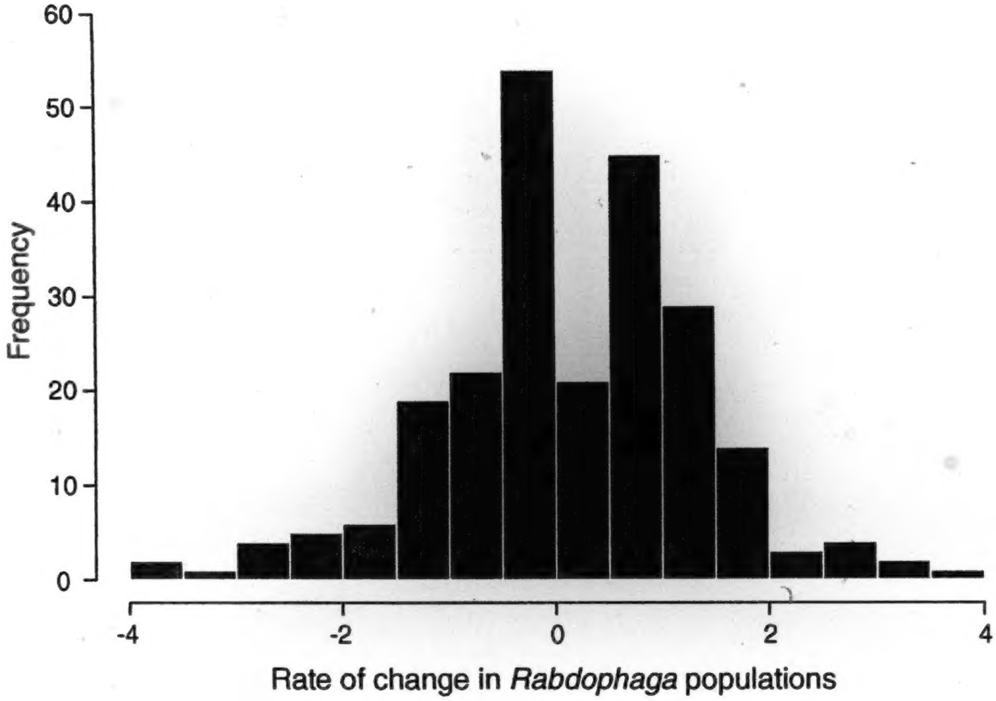

600
500
400
300
200
100
0
Northing (m)
0
100
200
300
400
500
600
Easting (m)

Figure 3-5. Variation in the rate of change in gall numbers (ln(N99)-ln(N98)) among the 232 willows in the study area.



Frequency
60
50
40
30
20
10
0
-4
-2
0
2
4
Rate of change in *Rabdophaga* populations

Figure 3-6. Best-fitting dispersal functions for a) the host, *Rabdophaga* and b) the parasitoids *Gastrancistrus* (open circles) and *Torymus* (filled circles). Each point indicates the expected proportion of individuals emigrating from willow-31 to other willows in the study area. Host dispersal was best described by a power function with a constrained proportion of emigrants (model 6). Parasitoid dispersal was best described by the negative exponential model with a constrained proportion of emigrants (model 5).

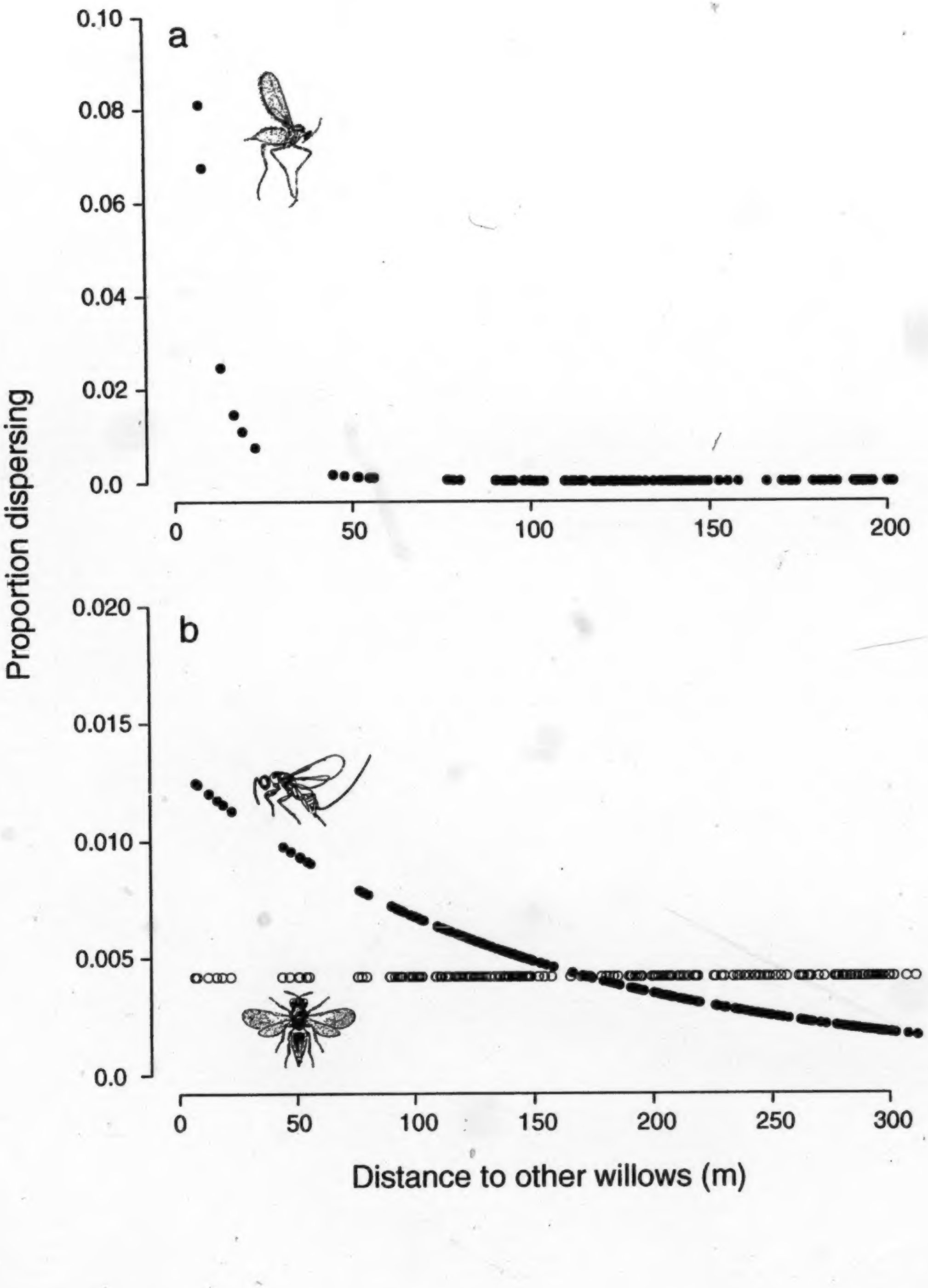

a
0.10
0.08
0.06
0.04
0.02
0.0
0
50
100
150
200
Proportion dispersing
b
0.020
0.015
0.010
0.005
0.0
0
50
100
150
200
250
300
Distance to other willows (m)

Figure 3-7. Comparison of model predictions and field observations for the number of a) Rabdophaga, b) *Gastrancistrus*, and c) *Torymus* on each of 232 willows in 1999. All values have been scaled using the transformation ln(x+1) to better show model deviations on willows where no individuals were observed.

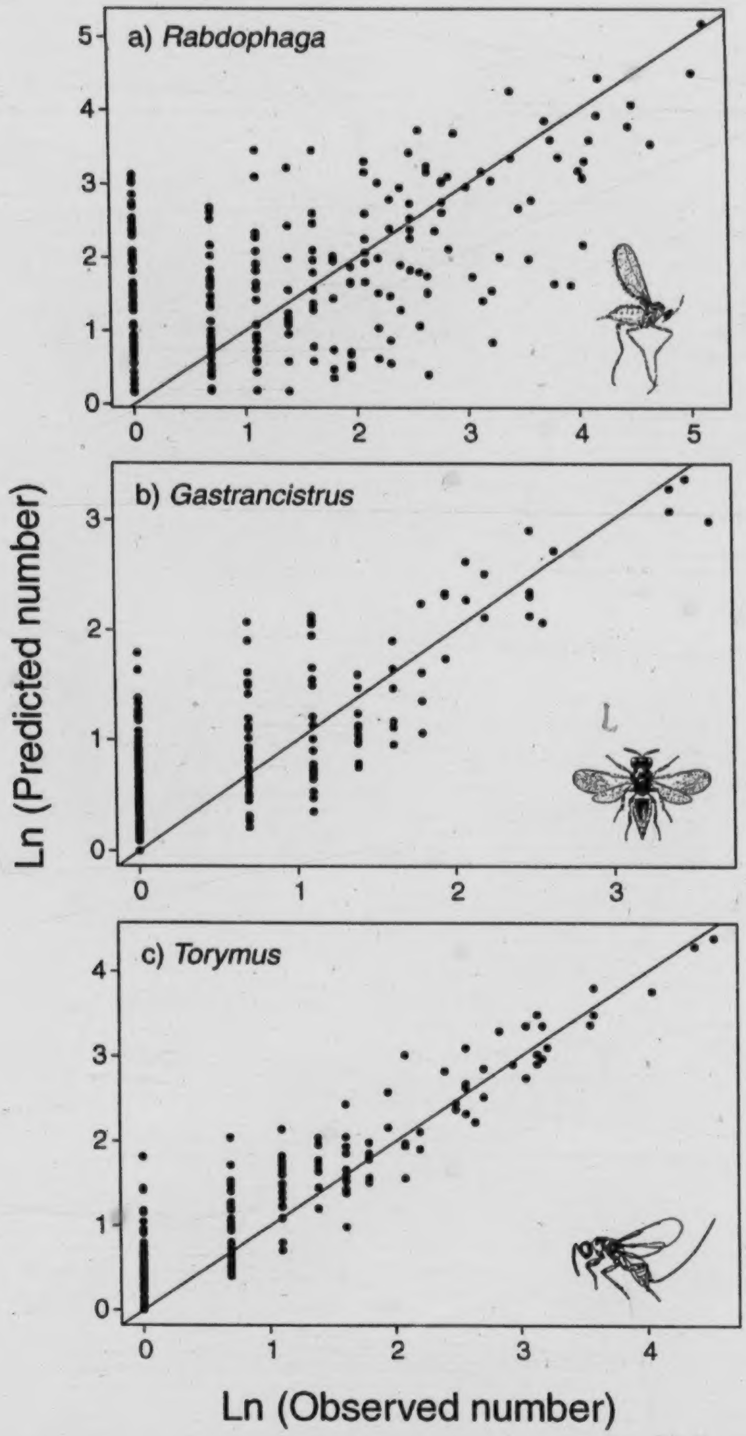
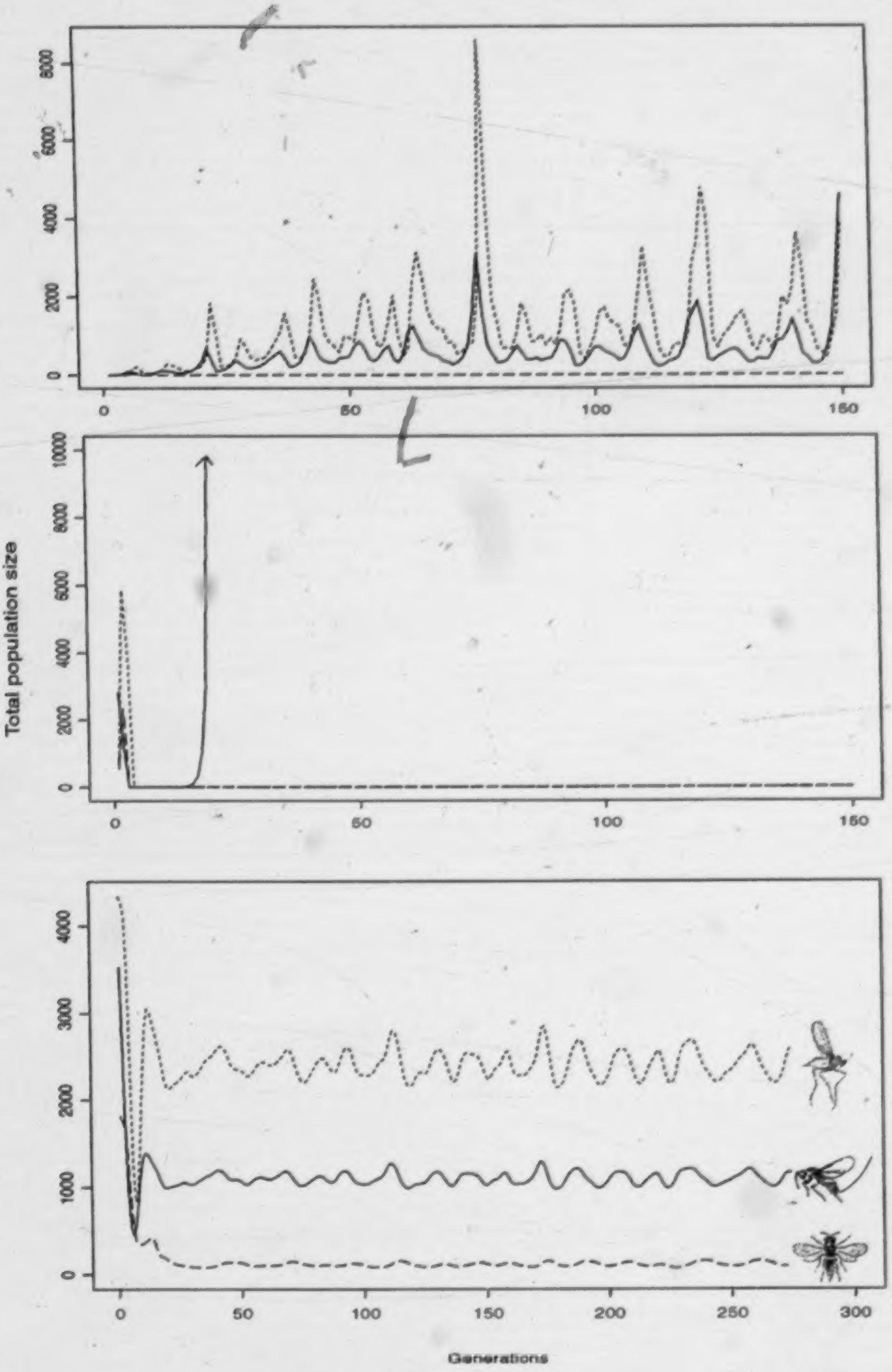

a) *Rabdophaga*
b) *Gastrancistrus*
c) *Torymus*
Ln (Predicted number)
Ln (Observed number)
0
1
2
3
4
5

Figure 3-8. Example ensemble time-series for simulations on a 30x30 lattice of habitat patches using a) the nearest-neighbour dispersal function, b) the best-fitting dispersal function for each species and c) the best fitting dispersal functions and among-willow variability in average gall diameter. Using nearest-neighbour dispersal, both the host *Rabdophaga* (dotted line), and the parasitoid *Torymus* (solid line), persist for 300 generations. *Gastrancistrus* (dashed line) becomes extinct in all patches with the first peak in *Torymus* numbers around the fifth generation. Using the best-fitting dispersal functions, *Torymus* rapidly colonises all patches, over-exploits its host and rapidly drives both *Gastrancistrus* and itself to extinction within ten generations. *Rabdophaga* is either driven to extinction as well or increases without bounds depending on the initial starting conditions. When among-willow variability in gall size is incorporated into the simulations, stable coexistence of all three species is achieved with abundances of each species qualitatively similar to those observed in the field.


8000
6000
4000
2000
0
0
50
100
150
10000
8000
6000
4000
2000
0
Total population size
0
50
100
150
4000
3000
2000
1000
0
0
50
100
150
200
250
300
Generations

Chapter 4:

Dynamics of a host-parasitoid community: The effects of spatial and temporal refuges on the coexistence of competing parasitoid species

INTRODUCTION

Gause's (1934) contention that two species with similar ecology cannot exist has sparked decades of debate surrounding what has come to be known as the principle of competitive exclusion (Hardin 1960). Early opponents (Cole 1960) dismissed it as an un-testable theory but conceded that competition will likely speed the extirpation of one of the species. As with any simple but general principle, it will inevitably be untrue for any real situation but can be very useful in guiding one in asking more informative questions.

Hutchinson (1951) first proposed the idea that competing species could coexist if the inferior competitor could disperse futher than the better competitor. This prompted a lively search for examples of such "fugitive" species (Armstrong 1976, Washburn & Cornell 1981, Hanski & Ranta 1983, Hopper 1984, Amarasekare 2000, van Nuyhous & Hanski 2002) and a search for other mechanisms that would allow the coexistence of competitors including spatial heterogeneity (Skellam 1951), spatial aggregation of parasitoids (Chesson & Murdoch 1986), stage-structured competitive interactions (Briggs 1993) and stochastic disturbances (Nee & May 1992). In these investigations the focus was on the effect that a particular process, such as dispersal, has on the ability of competing species to coexist. Theoretical studies (Comins & Hassell 1996, Wilson & Hassell 1997) have shown that dispersal in spatially structured habitats can allow competing parasitoids to coexist and also has more dramatic effects on the dynamics of populations through the generation of self-organising spatial patterns (Hassell Comins & May 1994). If the relative dispersal strategies of two species are related to the level of competition between them, selection should act on the inferior competitor to modify its dispersal rate such that competition is reduced. In this way, competition can be thought to affect the dispersal rates of at least one of the parasitoid species. and consequently the dynamics of the community. Thus, given the potential importance of dispersal on population dynamics, it may be useful to examine both dispersal and competition and how these processes interact.

Differences in dispersal rates between the host and its parasitoids can create spatial refuges for both the host and the disadvantaged competitor and it is well known that refuges can be an important stabilising mechanism in host-parasitoid interactions (Hassell 1978). In many internally feeding phytophagous insects, especially gall forming species, the plant tissues surrounding the insect is thought to afford some protection from natural enemies to the gall-former (Askew 1961, Price, Weis, Abrahamson & McCrea 1985, Fernandes & Waring 1987, Romstöck-Völkl 1990, Lampo 1994, Plantard & Hochberg 1998). For the willow pinecone gall midge, *R. strobiloides,* I found that gall size has a significant effect not only on the intensity of mortality from natural enemies but also on the type of mortality experienced by midges while in the gall (Chapter 2). For example, large galls are susceptible to parasitism by *Gastrancistrus* but not by *Torymus* nor to predation by birds. Therefore, large galls afford protection to *Gastrancistrus* from subsequent multiparasitism and predation. Gall size is affected in part by genetic and phenotypic characteristics of the plant (Price & Clancy 1986, Weis & Abrahamson 1986, Weis, Wolfe & Gorman 1989, Chapter 2, Table 2-2). Consequently, larger-scale variation in plant quality can translate into spatial patterning of refuges. The spatial distribution of refuges thus results from the interaction between the small-scale process associated with a parasitoid or predators response to a specific gall, and the larger-scale process of genetic and environmental influences on gall size.

Genetic, environmental, and stochastic factors can also interact to affect the temporal variability in gall diameter on a particular willow. Price & Clancy (1986) found that a very high temporal correlation in gall diameter among willow clones ($r^2 > 0.9$) was largely due to genetic factors but that drought also affected gall diameter substantially and reduced the correlation in gall diameter among years. Therefore, because of possible interactions between the temporal and spatial structure of refuges, and the dispersal rates of hosts and parasitoids occupying those refuges, assessing the dynamic effect of refuges can be quite complex. However, as has been argued by others (Price *et al.* 1980), understanding these interactions is critical for developing a robust understanding of the dynamics of such a community.

In this paper I explore how the processes of competition, dispersal, and gall-size induced refuges, interact spatially and temporally to affect the coexistence of parasitoid species of *R. strobiloides*. Due to the complexity of the problem I use a combination of experimental manipulations, detailed population censuses, and numerical simulations based on mechanistic host-parasitoid models. First I determine if, and to what extent, the species compete for hosts under field conditions averaged over time and space. Next, I determine if the two species differ in their dispersal abilities and how this affects their competitive interactions. I then use a spatially structured host-parasitoid model to describe the relationship between dispersal of each parasitoid species, and competition between the species. Lastly, I examine how temporal variability in gall size (refuge persistence) and variability in the magnitude of the gall-size effect (refuge distribution), both affect the co-existence of the two parasitoids.

Natural history of the host-parasitoid community

Rabdophaga strobiloides (Cecidomyiidae) is a univoltine and solitary bud-galling midge in North America (Gagné 1989), which at my study site in Alberta, Canada, forms galls predominantly on Bebb's willow, *Salix bebbiana* Sarg.

Adult midges emerge synchronously from galls in mid to late May. Females are mated within hours of emergence and lay eggs singly on the lower surface of leaves on expanding terminal shoots. Egg hatch occurs within 2-3 days, after which the first instar larva migrates to the apical meristem and begins feeding. Gall diameter increases throughout the summer (June – September) during which time the larvae pass through three instars. At my study site, galls reach their maximum size by September and at that time and range from 2.8 mm to 29.7 mm in diameter (mean = 13.84, n = 7184). Pupation occurs within the gall the following spring. After midges emerge, galls remain on the willows for up to four years.

In Alberta, *R. strobiloides* larvae are commonly attacked by two species of parasitoids. Adult female *Gastrancistrus* sp. (Hymenoptera: Pteromalidae) emerge from the previous generation of galls in June and attack new galls containing first instar midge larvae. These solitary koinobionts oviposit through the gall tissue and lay a single egg within the host larva. Galls are also parasitised by *Torymus cecidomyiae* (Walker) (=*strobiloides*) (Hymenoptera: Torymidae). These solitary idiobionts emerge from the previous year's galls in early August and attack the current year's galls when they have nearly reached their final size. Female *T. cecidomyiae* use their long ovipositor to deposit a single egg either on the midge larva or in the midge's larval chamber. Both parasitoid species remain within the gall during their larval and pupal stages. Although it is difficult to be certain that these parasitoids are strict specialists on *R. strobiloides*, there is no report in the literature of them being associated with any other hosts, nor have they been recovered from collections of galls of other species in the study area (personal observation).

METHODS

Description of study area and general methods

All the fieldwork was conducted at the Rumsey Ecological Reserve in central Alberta, Canada (51°55'N, 112°38W). The topography is characterised as 'knob and kettle' or hummocky where the landscape is dominated by a regular arrangement of hills and wet depressions. The vegetative community is primarily fescue prairie grassland dominated by *Festuca hallii* (Vasey) Piper, *Stipa* spp. and *Agropyron* spp., with patches of *Populus tremuloides* Michx., *Salix* spp. and *Rosa* spp. (Strong & Leggat 1992). The most common species of willows are *Salix petiolaris* J.E. Smith and *S. bebbiana* but galls of *R. strobiloides* have only been found on the latter at this site.

Two areas in the reserve were chosen for an experimental study of dispersal and an intensive life-table study, respectively. Within each of these, only those willows that produced at least one gall between 1996 and 1999 were identified as potential host plants. Willows were numbered and marked with permanent metal tree tags and their relative locations mapped with a precision of 0.5 m using 1:5000 aerial photographs. The 'experimental area' (Fig. 4-1) was approximately 30 ha in extent in which 388 individual Bebb's willows were identified. The 'reference area' used for the life-table studies (Fig. 4-1) was located 1.0 km west of the experimental area, was approximately 20 ha in extent, and contained 288 Bebb's willows.

I had previously identified gall diameter as an important determinant of both the intensity and type of mortality suffered by the gall midge while in the gall (Chapter 2). In the current study therefore, the diameter of each sampled gall was measured to the nearest millimetre with dial callipers. Measurements were taken at the widest part of the gall, perpendicular to the axis of the stem. The fate of each gall was determined by dissection in the laboratory. In the case of galls that were dissected before any insect emergence, development was allowed to proceed at room temperature until all insects had reached the stage of fully developed larva or pupa.

In these stages, parasitoid species were easily detected and identified. In the case of galls that were collected after insects had emerged in the field, gall fate was determined based on a suite of characters that are associated with each of the different sources of midge mortality (Appendix A).

Assessing competition for hosts between *Gastrancistrus* and *Torymus*

Both *Gastrancistrus* and *Torymus* are solitary parasitoids and as such, only one progeny of either species can be produced per host larva. In Chapter 2, I showed that *Torymus* larvae always kill *Gastrancistrus* larvae when they co-occur in the same host. Therefore, to assess the intensity of competition between these two species I measured the proportion of hosts that are attacked by each species alone, and the proportion of hosts that were attacked by both species contemporaneously. To do this I destructively sampled the population of galls in the reference area in December 1999 after all *Torymus* attacks were complete but before this species had developed beyond the second instar. At this stage, the internal *Gastrancistrus* larvae are also detectable in the host.

Measuring dispersal

Invasion ability

To obtain a direct estimate of the dispersal abilities of the host and the two parasitoid species I conducted a large-scale removal of galls from the experimental area and measured the patterns of re-invasion of all three species in the following two years. In April 1998, before any insects had emerged from the galls and before leaves had flushed, all the willows in the study area were surveyed and all galls were removed. The extent of the area that was known to be devoid of galls was marked on a map. In the spring of 1999, before any emergence, the area was re-surveyed. All galls that were found were clipped from the branches and then re-attached securely to the willows from which they had been clipped. This was done to allow a second generation of invasion during the summer of 1999 from the point to which they had successfully dispersed in 1998. As well, this minimised subsequent loss of galls in the field since the stems become brittle during the second year. In the fall of 1999, both the 1998-generation (re-attached galls) and the 1999-generation of galls (new galls) were collected and dissected in the laboratory. Therefore, the data used in following analyses were the number of galls on each willow, the number of parasitoids of each species within those galls, the diameter of each gall, and the shortest distance from each willow to the edge of the cleared area for both 1998 and 1999.

An additional 14 willows that surrounded the removal area were also surveyed. Galls found on these willows were collected. These galls were processed along with the galls in the removal area to control for any methodological biases in assigning gall fate in this control group.

The spatial patterns of abundance in the year following removal were described for each species using cubic B-spline functions relating the occurrence of hosts or parasitoids to the distance from the edge of the cleared area. Significant trends were identified using a randomisation procedure in which the distances were shuffled 1000 times and the spline function refit to these shuffled data (Noreen 1989). The observed trends were then graphically compared to the distribution of randomised fits to detect any deviations from a random distribution.

Patch colonisation ability

To measure the effect of isolation on the natural patterns of patch colonisation in the host and the two parasitoid species I used census data for the reference area from 1997 through 1999 and from the experimental area from 1996 through 1999. These data consisted of counts of galls on each willow in the respective area, the gall diameters, and their fate. Individual willows were treated as patches for this analysis because preliminary surveys indicated that it was at this scale that local extinctions tended to occur. Successful colonisation was defined as occurring when a species was absent from a patch in one year and present in the same patch the next year. For parasitoids, patches that did not have any hosts were excluded from the analysis. The isolation of each patch was estimated as the sum of the distances to the four nearest neighbouring patches (NN4) and the sum of the distances to the 30 nearest neighbours (NN30). These two values assess isolation at two different spatial scales and were chosen because I had no a priori expectation of how the colonisation of patches was affected by isolation.

Data from the experimental area were used to check the robustness of the analysis of patch colonisation. In the year before the removal, it was expected that the distance to neighbouring patches could influence the colonisation of a particular patch. In the first year following the removal no relationship was expected between patch colonisation and isolation from neighbouring patches since none of these contained source populations. Patch colonisation in 1999 was expected to be related to the distance to the edge of the cleared area or related to the distance to neighbouring patches, depending on how rapidly insects recolonised the cleared area in 1998.

In previous experiments where mature galls were transplanted onto *S. petiolaris* I found that emerging midges are able to identify *S. petiolaris* as an unsuitable host plant and lay fewer eggs on this species compared to *S. bebbiana*. Based on this finding, I suspected that the amount of non-host vegetation surrounding *S. bebbiana* might affect the realised isolation of each patch. To incorporate this into the analysis I classified the vegetation around each patch using 1:5000 aerial photographs combined with ground surveys. Vegetation was classified as grassland, non-host willow (mainly *S. petiolaris*), and aspen (*P. tremuloides*). The amount of non-host willow was calculated at three spatial scales as the area of land covered by that vegetation class as a proportion of a square area 4x4 m (PET4), 20x20 m (PET20), and 40x40 m (PET40) centred on each patch.

The effect of isolation and non-host willow on the probability of colonisation was analysed using a generalised linear model (GLM) with binomial errors and a logit link function in S-plus 2000. A separate model was calculated for each insect species and each year. The best-fitting models were identified using a stepwise procedure based on the *Cp* statistic (Spector 1994, S-plus 2000). If model errors were determined to be substantially over-dispersed (making significance tests too liberal), the quasi-likelihood option was used to scale the dispersion parameter (McCullagh & Nelder 1989). Once the best fitting model was identified, individual parameters were tested for statistical significance using analysis of deviance (McCullagh & Nelder 1989).

Measuring the effect of dispersal on host-use overlap

For the 1999 generation of parasitoids, I could estimate both the amount of host-use overlap from dissections, as well as the dispersal rates of the parasitoid species. If *Gastrancistrus* is adapted to avoid competition with *Torymus* by adopting a particular dispersal strategy (for example, out-running its competitor), then I would expect that any substantial change in its dispersal strategy would result in greater host-use overlap, and consequently, poorer survival of *Gastrancistrus* offspring. To determine if *Gastrancistrus'* observed dispersal strategy in fact minimises host-use overlap with *Torymus,* I used the spatially explicit growth-dispersal model developed for the reference area in the previous chapter (eqn 7, Chapter 3) and simulated host-use for both parasitoids under a variety of alternative dispersal strategies. I used the real spatial arrangement of willows in the experimental area and the corresponding abundance data in 1998 as a starting point for the model. For each run of the model I used a different set of dispersal parameters for each of the parasitoids to calculate the spatial distributions of parasitoid attacks for the 1999-generation.

Host-use overlap was measured as the proportion of hosts that were multiparasitised; hosts that were attacked by both species. The rate of multiparasitism (*M*), was calculated using the following equation:

$$M = \gamma_P \, [1 - f_1(P_t)] \, \gamma_Q \, [1 - f_2(Q_t)] \qquad \text{eqn 1}$$

where γ_P and γ_Q are the proportion of hosts susceptible to parasitism by *Gastrancistrus* and *Torymus* as a result of gall-size effects (Chapter 2) and where $f_1(P_t)$ and $f_2(Q_t)$ are the functions that describe the proportion of hosts attacked by *Gastrancistrus*, and *Torymus* respectively. Thus, because *Gastrancistrus* is always killed in multiply parasitised hosts, *M* represents direct reproductive costs associated with a particular dispersal strategy. In the interpretation of the results of this simulation I focus on the effect that *Gastrancistrus* dispersal has on multiparasitism rates conditional on the dispersal strategy used by *Torymus,* to emphasise the asymmetric nature of their interaction.

The dispersal of each parasitoid species is described by two parameters, μ, the proportion of female parasitoids in a patch that emigrate to other patches and δ, the rate at which the number of dispersers moving from the natal patch to another patch decreases with increasing distance (Chapter 3). Each of these parameters can vary between 0 and 1.0 and therefore precisely describing the response surface can potentially involve many calculations. To reduce the number of computations, I first used parameters ranging from 0 to 1.0 with intervals of 0.1 and only one replicate run for each combination of parameter values. After determining the general shape of the surface and concluding that there were no abrupt changes, I reduced the number of intervals in order to permit a larger number of replicate runs.

For each run of the model I used a different distribution of gall diameters obtained by sampling from the 1999 distribution with replacement. I did this to make the results of these simulations insensitive to any particular distribution of gall diameters. To reduce the variability in model output due to randomly chosen gall diameters, I replicated model runs 100 times for each combination of dispersal parameters and then calculated an average value of multiparasitism M for each run.

Assessing the effect of gall-size refuges on coexistence

Temporal variability

In the *R. strobiloides* community, refuges are created as a result of differences in the response to variation in gall size among the natural enemies. Therefore, the persistence of refuges through time can be described as persistence in the distribution of gall sizes through time. If the average size of galls on a willow changes unpredictably between years, the potential of this willow as a refuge for *Gastrancistrus* might be diminished. Previous work (Chapter 2, Table 2-3) has found that the correlation in average gall size between years is 0.31, on average. To examine the effect of temporal variability in gall size (refuge persistence) on the ability of *Gastrancistrus* to coexist with *Torymus*, I simulated the host-parasitoid dynamics using the previously-described spatially structured model. In the simulations I varied the temporal variability in average gall size, while holding other parameters constant. This allowed me to determine how temporal variability alone affected the coexistence of the two parasitoid species.

As in the previous section, I used the parameterised growth-dispersal model from Chapter 3 but for these simulations I made three modifications. In order to simulate multiple generations, I needed to include other sources of midge and parasitoid mortality that had been methodologically removed in the parameterisation of the model. I included over-winter predation by applying the observed size-dependent bird predation rates from the experimental area in 1997 to the simulated population of galls in each generation. Bird predation was assumed to occur after, and independent of, all other sources of larval mortality. The 1997 predation rates were used because no manipulations had yet occurred in the experimental area in that year, and some sampling bias was suspected in the 1996 data. 'Other' sources of mortality, as defined in Chapter 2, were similarly incorporated into the model. The observed size-dependent mortality rates from the experimental area from 1998 were used in this case because the patterns of mortality did not differ significantly among years (Chapter 2) and because the 1998 cohort had the best representation of galls in the tails of the size distribution (Fig. 2-2, Chapter 2).

In addition to adding bird predation and other sources of mortality I also modified the model to incorporate a temporal correlation in gall diameters. The typical way to add temporally correlated variability is to generate serially autocorrelated and normally distributed errors to a constant mean gall size (Royama 1992). Over the ensemble of patches this generates a distribution of gall sizes converging on a normal distribution. Because galls cannot be infinitely large or small this distribution must be truncated at the tails. This method was tried but the resulting distribution of gall sizes still did not match the observed distribution very well. Furthermore, preliminary trials indicated that the simulation model was particularly sensitive to changes in the shape of the gall size distribution. To avoid these problems I developed a method of generating temporally correlated average gall sizes that maintained the observed distribution of average gall sizes among willows (Appendix 4-A).

Using the complete model formulation I simulated the population trajectories of all three species using the 1998 populations in the experimental area as a starting point for each run of the model. Trajectories were simulated across the range of temporal variability from a correlation of 0, completely random fluctuations in average gall size through time, to 1.0 representing constant average gall size through time. Simulations were repeated 20 times for each level of temporal correlation in gall size and the mean number of generations that both parasitoid species persisted was calculated. Persistence was defined as occurring when the total number of individuals across the 388 patches was greater than one.

Spatial variability

Differential responses of parasitoids and predators to variation in gall size results in size-dependent refuges that differ for both the host and each of the parasitoid species

(Chapter 2). Due to variation in the average gall diameter among willows, the refuges created by galls can exhibit spatial variability. For example, if willow genotypes affect gall diameter strongly, one might expect a fine-grain patterning of refuges over the study area. Conversely, if gall size is largely determined by environmental factors such as water availability, one might expect a more coarse-grained structure to the distribution of refuges because these types of factors would likely be correlated at larger spatial scales than willow genotypes. To examine the effect of the spatial variability of refuges on the co-existence of the two parasitoid species I used a modelling technique similar to that in the previous section. From a mechanistic point of view it would seem most reasonable to control spatial variation in gall size, and consequently variation in refuges. This approach is inappropriate however, because then one must arbitrarily choose a mean gall diameter and the type of refuge (a refuge for *Gastrancistrus* from *Torymus* vs. a refuge for *Torymus* from bird predation) depends critically on gall diameter. Instead, I varied the intensity of the *response* of the parasitoids to gall size. To illustrate this consider the extreme case where parasitoid attack rates are simulated to be unrelated to gall size. Here, the refuge (or the absence of a refuge) is effectively the same everywhere in the population irrespective of any spatial variation in gall diameter. At the other end of the spectrum, if the attack rates of parasitoids are very sharply defined by gall diameter, then refuges will consequently be quite variable in space.

To vary the response of parasitoids to gall size in the simulations I started with the patterns of attack that were described for each of the midge's mortality factors in

Chapter 2. Using the same rationale as in Chapter 3 the attack rates were scaled up such that the maximum attack rate was taken to represent a susceptibility value of 1.0 (entirely susceptible to parasitism). These functions were then 'flattened' by dividing them by a factor *F*. Larger values of *F* result in a decreased response of the parasitoids to gall diameter, low values of *F* represent responses that are closer to the observed responses (*F*=1). Lastly, the intercepts of the functions were adjusted such that the same overall level of susceptibility to parasitism was the same for each of the functions (Figure 4-2); in this way the mean response stays the same and only the strength of the response varies.

Simulations were conducted using 1998 populations in the experimental area and the spatial locations of the 388 willows as a starting point for each run of the model. Simulations were run over a series of values of *F* ranging from 1.0 (observed variation in the response of parasitoids to gall diameter) to 100 (no variation). Model runs were replicated 20 times and the mean number of generations that both parasitoid species persisted was calculated.

RESULTS

Competition for hosts between *Gastrancistrus* and *Torymus*

From a random sample of 45 willows in the reference area in 1999, a total of 561 galls were dissected before parasitoid development was complete. Of the 377 galls in this sample that were parasitised by at least one species, 34% were parasitised by

Gastrancistrus alone, 48% by *Torymus* alone, and 17% by both species. Of the 196 galls that were parasitised by *Gastrancistrus*, 34% were also attacked by *Torymus* and the rate of multiparasitism decreased with increasing gall diameter (Fig. 4-3) suggesting that large galls act as a refuge for *Gastrancistrus*. To check that *Torymus* was competitively dominant in this cohort, a sample of 1289 galls were dissected after parasitoid development was complete. In this sample, 883 galls were parasitised and of those, 28% were parasitised by *Gastrancistrus* alone and 71% by *Torymus* alone. This suggests that all of the *Gastrancistrus* larvae in multiparasitised galls eventually succumb to *Torymus*.

Dispersal

Invasion ability

There was no significant relationship between abundance of any of the three species and distance from the edge of the cleared area in the year prior to experimental removal (1997, Fig. 4-4 to 4-6). This pattern confirmed that there was no gradient in host abundance or parasitism rates across the study area prior to the experiment that could generate a spurious distance effect.

In the first year after removal (1998), the abundance of *Rabdophaga* was again independent of distance (Fig. 4-4) and total abundance of the midge was similar to that in the year preceding manipulation ($n = 2337$ in 1997 and $n = 2017$ in 1998). For *Gastrancistrus* there were significant departures from randomness although the pattern is not consistent with distance to the edge (Fig. 4-5). Parasitism by

Gastrancistrus was higher than expected near the edge of the clearing, lower than expected between 100 m and 200 m, and approximately average beyond 200 m. The abundance of *Torymus* declined with distance from the edge (Fig. 4-6, $P < 0.001$) and total rates of parasitism were reduced relative to the reference willows outside the removal area. (23.4% vs. 22.5% for 1997 and 7.6% vs. 26.6% for 1998). The decline in parasitism was most evident at distances beyond 200 m, although the relationship was not strongly non-linear.

In 1999, the year following removal, there was, again, no relationship between distance from the edge of the clearing and the abundance of any of the species.

Patch colonisation ability

Within the experimental area, colonisation of empty patches by *Rabdophaga* was consistently affected by the amount of *S. petiolaris* surrounding each patch but not by the distance to neighbouring *S. bebbiana* patches (Table 4-1). However, the effect of surrounding vegetation differed substantially between the time before and after the experimental removal. The colonisation of patches was positively affected by the PET20 in 1997 (pre-manipulation), negatively affected by PET40 after the removal in 1998 and negatively affected by PET20 in 1999 (Table 4-1). In the neighbouring reference area, PET20 had a significant positive effect on colonisation in 1998 (like the pattern in the pre-removal plots), and the distance to the four nearest neighbours (NN4) had a weak negative effect on colonisation in 1999.

In all years in the experimental area, colonisation by *Gastrancistrus* was affected only by the number of galls in a patch (Table 4-2). Neither the degree of isolation nor the amount of surrounding non-host willow had an effect on colonisation by this parasitoid. In the reference area, the only significant predictor of colonisation was the amount of *S. petiolaris* at the 40m-scale in 1999 with declining patch colonisation where there was more *S. petiolaris* surrounding the patch.

Within the experimental area, colonisation by *Torymus* in all years was significantly and positively affected by the number of galls in a patch, in that year (Table 4-3). Furthermore, gall number within patches explained the greatest amount of variation in *Torymus* colonisation. The degree of isolation, when measured as the total distance to the four nearest neighbours (NN4), had a negative effect on the chance of *Torymus* colonisation in 1997 and 1999 but not in 1998; generally, willows further from a source were less likely to be colonised. The magnitude of the effect of isolation was similar in 1997 and 1999 suggesting that the system had equilibrated to 'pre-removal' condition within the two years. The total distance to the thirty nearest neighbours (NN30) was not a significant predictor of colonisation in any year suggesting that isolation effects tend to be local. The amount of non-host willow measured at the 4 m scale (PET4) had a positive effect on *Torymus* colonisation in 1997 but not in the other years nor when measured at larger scales. In the reference area the patterns of colonisation by *Torymus* were similar to the experimental area but statistical significance was generally lower, likely due to the smaller area and reduced number of willows. Colonisation by *Torymus* was higher in patches with more galls in both

1998 and 1999, and in the less isolated patches (NN4) in 1998 ($P = 0.055$). No effect of isolation was detected in 1999.

The effect of dispersal on host-use overlap

When the dispersal rate of *Torymus* is low (Fig. 4-7 a,c,e), *Gastrancistrus* can always increase its fitness (decrease the rate of multiparasitism) by increasing its dispersal rate (eg. $\mu_{Gast} = 0$ vs. $\mu_{Gast} = 1$). However, the magnitude of this effect is very small reducing rates of multiparasitism by only 1%. Similarly, altering the average dispersal distance of *Gastrancistrus* (δ_{Gast}) had very little effect on host-use overlap.

When the dispersal rate of *Torymus* is high (Fig. 4-7 b,d,f), *Gastrancistrus* can always reduce host-use overlap by decreasing its dispersal rate (different lines in each panel). When *Torymus* had a high dispersal rate but dispersed locally (Fig. 4-7b), *Gastrancistrus* could reduce host-use overlap by dispersing more widely (increasing values along the x-axis). Conversely, when *Torymus* dispersed widely (Fig. 4-7f), the best strategy for *Gastrancistrus* was to disperse locally.

In general, model simulations produced predictions that were consistent with the observed rates of multiparasitism. Using the best-fitting parameter estimates for the growth-dispersal model (Chapter 3, Tables 3-2 - 3-4), the model predicts that 9.5% of the parasitised hosts in 1999 contain both species of parasitoids. Surprisingly, this suggests that the dispersal patterns estimated for *Torymus* and *Gastrancistrus* result in nearly maximal rates of host-use overlap.

Refuges and coexistence

Temporal variability

Correlation in the average gall size between years (refuge persistence) had a significant impact on the number of generations that the two parasitoid species were able to coexist (Fig. 4-8). When the average gall size for a given willow is not correlated through time ($r < 0.1$), coexistence of the two parasitoids never lasted beyond four generations. When gall size for a given willow was correlated through time ($r > 0.3$), some runs of the simulations resulted in coexistence for up to 200 generations but the variability between runs was high and most resulted in the extinction of *Gastrancistrus* in less than 50 generations. When willows producing large galls always produce large galls ($r > 0.9$), refuges are very stable and coexistence generally occurred for more than 100 generations. Therefore, the temporal correlation in gall size observed in the field study ($r = 0.31$, Table 2-3), may be sufficient to allow coexistence of the parasitoid species but other factors likely contribute.

Spatial variability

The simulations suggest that the long-term coexistence of both parasitoids depends on spatial variability in refuges caused by the effect of gall size on the patterns of attack by the parasitoids (Fig. 4-9). Coexistence was maintained even when variability in refuges was decreased 8-fold. However, further decreases in variability resulted in a significant decline in the average number of generations of coexistence. In all cases where *Gastrancistrus* and *Torymus* did not coexist for up to 200 generations, it was *Gastrancistrus* that was extirpated first.

DISCUSSION

From the detailed censuses of both study areas, from the general surveys across the Rumsey Ecological Reserve, and from more extensive collections throughout central Alberta, both *Gastrancistrus* and *Torymus* are always found in close proximity, and often in galls from the same willow bush. This local and regional coexistence sets the stage for potential conflict since both species are restricted to the same resource (*Rabdophaga* larvae) for reproduction. In fact, I have shown that a significant portion of the *Gastrancistrus* population is indeed killed by direct interference competition with *Torymus*, and that in a habitat without any spatial or temporal refuges from multiparasitism, *Gastrancistrus* cannot persist. Interestingly, even though *Gastrancistrus* and *Torymus* seem to differ in their dispersal abilities, variation of this parameter, in the model at least, does not appreciably affect the amount of competition between them.

How does gall size affect the coexistence of parasitoids?

The most parsimonious explanation for the observed patterns of coexistence is that variation in gall size provides a refuge for *Gastrancistrus* as evidenced by the decreasing rate of multiparasitism with increasing gall diameter (Fig. 4-3). On individual willows with many galls, a certain fraction of galls permit parasitism by *Gastrancistrus* but exclude *Torymus* because of their size. Both proportional and fixed-size refuges can provide stability in host-parasitoid models (Hassell 1978) but this result assumes both temporal and spatial homogeneity. Given that gall-size refuges vary in time and space, it is not clear from existing theory how they contribute to the coexistence of the parasitoids.

Simulations presented here also suggest that the refuges created by variation in gall size are a necessary, but not sufficient condition for coexistence (Fig. 4-9). Due to the stochastic nature of the simulated *Rabdophaga* populations, all patches eventually contain only galls of a size that are susceptible to parasitism by both species. Therefore, what is also required for persistence is a minimum level of temporal correlation in the average gall size within patches (Fig. 4-8). This allows local populations of *Gastrancistrus* to do particularly well in a subset of patches that are not suitable for *Torymus*. Because gall size clearly varies through time, refuge patches will eventually disappear. Thus, some amount of between patch dispersal is also necessary.

Can differential dispersal mitigate competition within Rabdophaga galls?

Although dispersal may be necessary for the colonisation of new suitable patches, it may also reduce the competition for hosts between parasitoid species. Excluding other possible mechanisms of coexistence, the differential dispersal theory predicts that for the poorer competitor to persist in the community it must be a substantially better disperser (Levins & Culver 1971, Hastings 1980, Tilman 1994, Nee & May 1992, Hassell, Comins & May 1994). I found that, on average, one third of hosts that are parasitised by *Gastrancistrus* larvae are also parasitised by *Torymus* larvae and that *Gastrancistrus* larvae are at a distinct competitive disadvantage. The analyses of patch colonisation rates (Tables 4-2 & 4-3) and the invasion of the experimentally cleared area (Fig. 4-4) show that the two parasitoids differ in their dispersal abilities and that, consistent with theoretical predictions, the superior competitor, *Torymus,* is indeed the poorer disperser. However, the observed differences were significantly less than the ten-fold difference in dispersal rates thought to be needed for coexistence in spatially structured host-parasitoid models (Hassell, Comins & May 1994).

When the relationship between differential dispersal and the effect it has on host-use overlap was modelled using the real spatial arrangement of patches, it was evident that even substantial differences in dispersal strategies resulted in only modest differences in host-use overlap (Fig. 4-7). As well, given the ubiquitous distribution of *Torymus* in what appears to be a well connected patch network, the best strategy for *Gastrancistrus*, to minimise its interaction with *Torymus*, is to disperse very little and only locally (Fig. 4-7e). However, even under this scenario, rates of multiparasitism are only reduced to 7% from a maximum possible of 10% when *Gastrancistrus* disperses evenly across all patches. This extreme case points to one pitfall of using rates of multiparasitism as a surrogate for fitness. Clearly the small competitive advantages of a 'no-dispersal' strategy would be offset by other disadvantages. For example, due to the stochastic nature of the often small *Rabdophaga* populations on individual patches, a female *Gastrancistrus* will frequently find herself in a patch without mates, or more seriously, without hosts. Not dispersing in these situations would undoubtedly have large fitness costs.

In general, the results of this study suggest that variation in gall size, and the refuges that result, are more important in reducing the competitive interactions between *Torymus* and *Gastrancistrus* than is differential dispersal. These results agree with the few other studies examining the effects of local versus spatial mechanisms on the coexistence of competing parasitoid species. Hopper (1984), through a combination of field experiments and greenhouse observations found that the density of five parasitoid species attacking *Rhopalomyia californica* was correlated with variation in searching efficiency. Briggs & Latto (2000), also working with *R. californica*, showed experimentally that dispersal among bushes synchronised the dynamics of sub-populations and that some dispersal was necessary for parasitoid coexistence, however, it was variation in searching efficiency at the local scale that had the biggest impact on parasitoid coexistence. Amarasekare (2000) found that coexistence of two specialist egg parasitoids was best explained by variation in host productivity and found no evidence for dispersal as a potential mechanism for mitigating competition.

All of these studies, including this one, were conducted at small to medium spatial scales (<1.0 km in extent). In contrast, large-scale investigations (6-70 km) of the metapopulation dynamics of *Melitaea cinxia* and its two specialist parasitoids provide evidence for differential dispersal as a mechanism promoting coexistence (Lei & Hanski 1998, van Nouhuys & Hanski, *in press*). In the *M. cinxia* community there is ample evidence that the host species acts as a classic metapopulation (Hanski, Kuussaari & Nieminen 1994). This large-scale spatial and temporal variability in host density likely has more pronounced effects on the distribution of the parasitoid species. It is currently unclear whether variability at this scale is common for other host-parasitoid communities.

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Table 4-1: Generalised linear models of the effect of landscape on the colonisation of unoccupied willows by *Rabdophaga strobiloides*. The predictive variables tested were the proportion of area covered by *Salix petiolaris* in a 4, 20, and 40m^2 area around each willow (PET4, PET20, PET40), and the total distance to the 4 and 30 nearest neighbouring willows (NN4, NN30).

Experimental area		Df	Coef.	S.E. Coef.	t	Explained Deviance	Resid. Df	Resid Deviance	P (Chi square)	Dispersion
1997										
	Null						263	365.739		
	PET20	1	2.250	1.016	2.214	34.176	262	331.563	0.000	1.26
	PET4	1	0.817	0.533	1.532	2.354	261	329.210	0.125	
1998										
	Null						184	254.900		
	PET40	1	-2.727	1.198	-2.276	5.300	183	249.600	0.021	1.36
1999										
	Null						193	231.339		
	PET20	1	-2.253	0.757	-2.976	9.165	192	222.174	0.002	1.16
Reference area										
1998										
	Null						161	216.512		
	PET20	1	2.913	1.001	2.912	9.642	160	206.870	0.002	1.29
1999										
	Null						101	125.287		
	NN4	1	-0.0035	0.0028	-1.956	4.197	100	121.090	0.040	1.21

Table 4-2: Generalised linear models of the effect of landscape on the colonisation of unoccupied willows by *Gastrancistrus* sp. The predictive variables tested were the total number of galls in the colonisation (GALLS97, GALLS98, GALLS99), the proportion of area covered by *Salix petiolaris* in a 4, 20, and 40m^2 area around each willow (PET4, PET20, PET40), and the total distance to the 4 and 30 nearest neighbouring willows (NN4, NN30).

Experimental area	Df	Coef.	S.E. Coef.	t	Explained Deviance	Resid. Df	Resid Deviance	P (Chi square)	Dispersion
1997									
Null					-	147	134.4337		
GALLS97		0.0257	0.0107	2.404	5.533	146	128.9002	0.019	0.88
1998									
Null						171	193.4433		
GALLS98		0.0571	0.0164	3.490	14.809	170	178.6347	0.0001	1.05
1999									
Null						203	280.427		
GALLS99	1	0.0195	0.0094	2.071	4.659	202	275.768	0.031	1.37
Reference area									
1998									
Null						84	104.680		
PET40		3.445	2.389	1.442	2.083	83	102.597	0.149	1.24
1999									
Null						122	164.538		
PET20		8.453	2.945	2.870	1.262	121	163.277	0.261	
PET40		-15.010	5.532	-2.713	8.901	120	154.376	0.003	1.28

Table 4-3: Generalised linear models of the effect of landscape on the colonisation of unoccupied willows by *Torymus cecidomyiae*. The predictive variables tested were the total number of galls in the colonisation year (GALLS97, GALLS98, GALLS99), the proportion of area covered by *Salix petiolaris* in a 4, 20, and 40m^2 area around each willow (PET4, PET20, PET40), and the total distance to the 4 and 30 nearest neighbouring willows (NN4, NN30).

Experimental area	Df	Coef.	S.E. Coef.	t	Explained Deviance	Resid. Df	Resid Deviance	P (Chi square)	Dispersion
1997									
Null						201	273.581		
GALLS97	1	0.249	0.047	5.268	57.805	200	215.776	0.000	
NN4	1	-0.0069	0.0028	-2.476	9.944	199	205.833	0.002	
PET4	1	1.068	0.496	2.155	3.924	198	201.909	0.048	
NN30	1	0.00016	0.00011	1.443	2.112	197	199.797	0.146	1.01
1998									
Null						71	76.278		
GALLS98	1	0.165	0.060	2.753	11.042	70	65.236	<0.001	0.93
1999									
Null						143	144.669		
GALLS99		0.296	0.085	3.487	32.669	142	112.000	0.000	
NN4		-0.00508	0.00210	-2.422	6.900	141	105.100	0.009	0.75
Reference area									
1998									
Null						65	85.339		
GALLS98		0.175	0.052	3.340	25.948	64	59.391	0.000	
NN4		-0.0199	0.0100	-1.978	3.675	63	55.716	0.055	
NN30		0.00041	0.00026	1.610	2.836	62	52.880	0.092	0.85

1999								
Null					84	111.533		
GALL99	0.592	0.142	4.157	50.003	83	61.531	0.000	0.74

Figure 4-1. Reference (top) and experimental (bottom) study areas in the Rumsey Ecological Reserve in central Alberta, Canada. Solid black lines delineate the extent of the study areas. Solid black circles indicate individual *Salix bebbiana*. Areas of *S. petiolaris* are stippled grey. White areas are unclassified vegetation, predominantly composed of grasses.

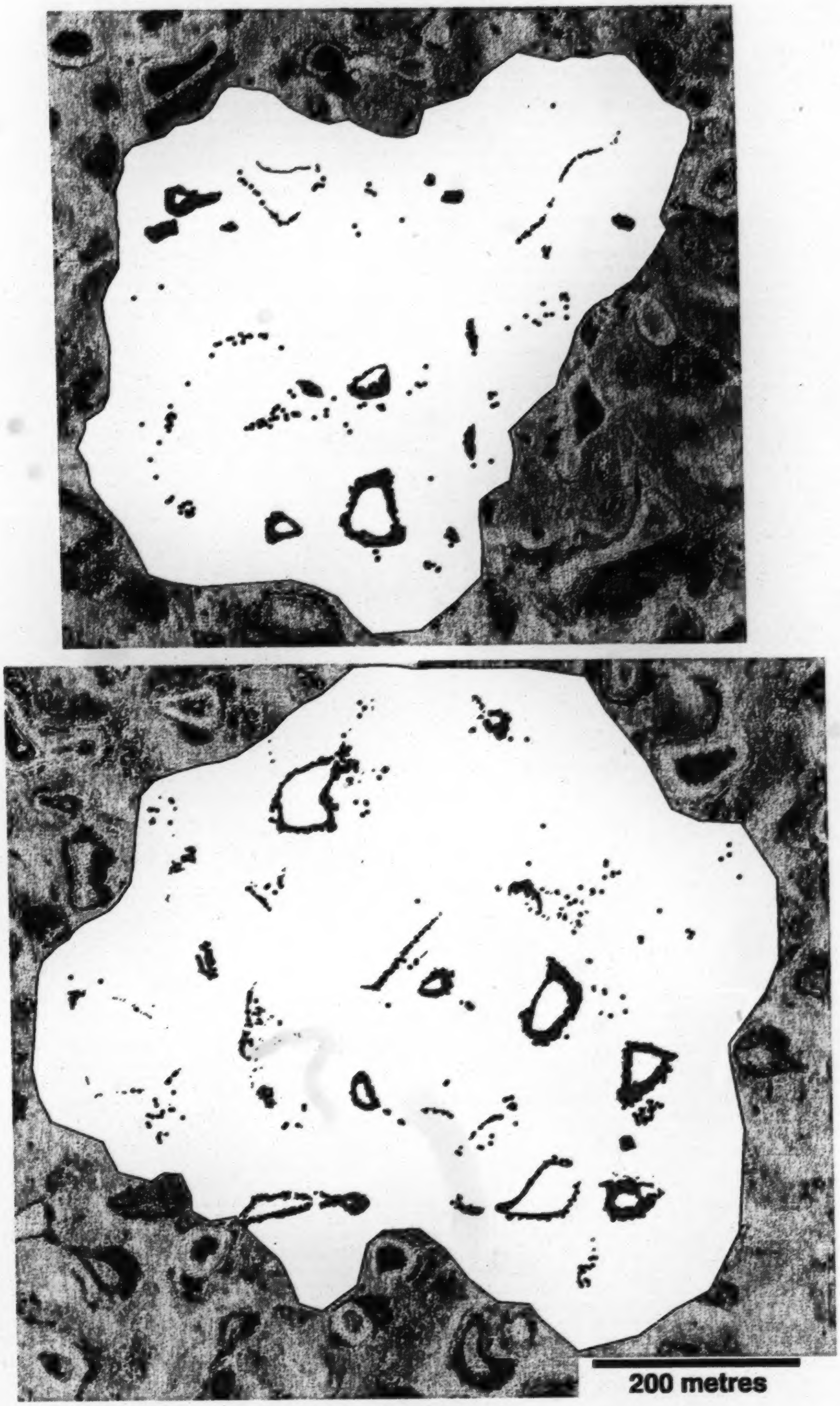

200 metres

Figure 4-2.Functions describing the susceptibility of galls to parasitism by *Torymus strobiloides* (top panel) and *Gastrancistrus* sp. (bottom panel) A value of $F = 1.0$ (lowest curve) represents the empirical susceptibility. Greater values of F decrease the range of susceptibility.

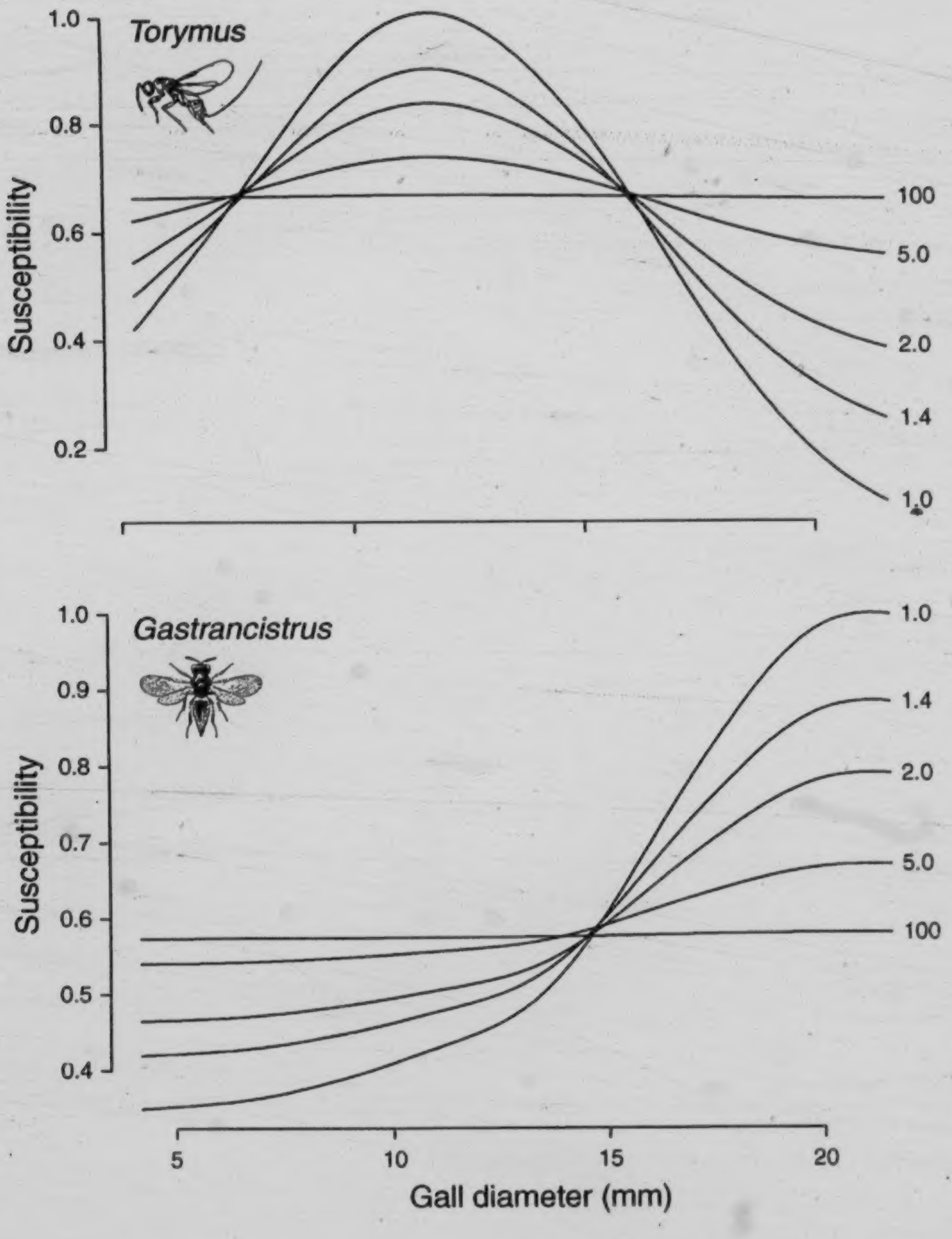

Torymus
1.0
0.8
0.6
0.4
0.2
Susceptibility
100
5.0
2.0
1.4
1.0
Gastrancistrus
1.0
0.9
0.8
0.7
0.6
0.5
0.4
Susceptibility
1.0
1.4
2.0
5.0
100
5
10
15
20
Gall diameter (mm)

Figure 4-3. Rates of multiparasitism as a function of gall diameter. Each point represents the proportion of galls in a given diameter class attacked by *Gastrancistrus* that were subsequently attacked by *Torymus*. Points are placed at the midpoint of the size class and size classes represented by less than five galls are indicated by an asterisk (Total $n = 196$).

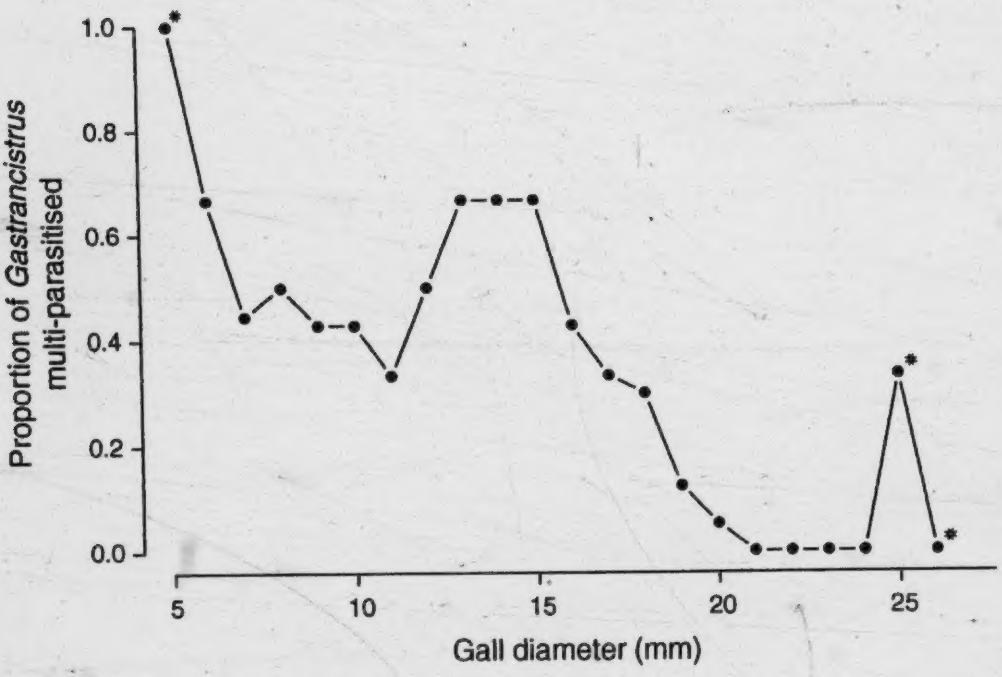

Proportion of *Gastrancistrus* multi-parasitised
1.0
0.8
0.6
0.4
0.2
0.0
Gall diameter (mm)
5
10
15
20
25
*
*
*

Figure 4-4. Relative abundance of *Rabdophaga strobiloides* galls as a function of the distance to the edge of the cleared area. The observed distribution (solid black line) was determined by fitting a nonparametric cubic B-spline to incidences of galls on individual willows using a generalised additive model. Grey lines represent functions generated by assuming randomly distributed galls among willows.

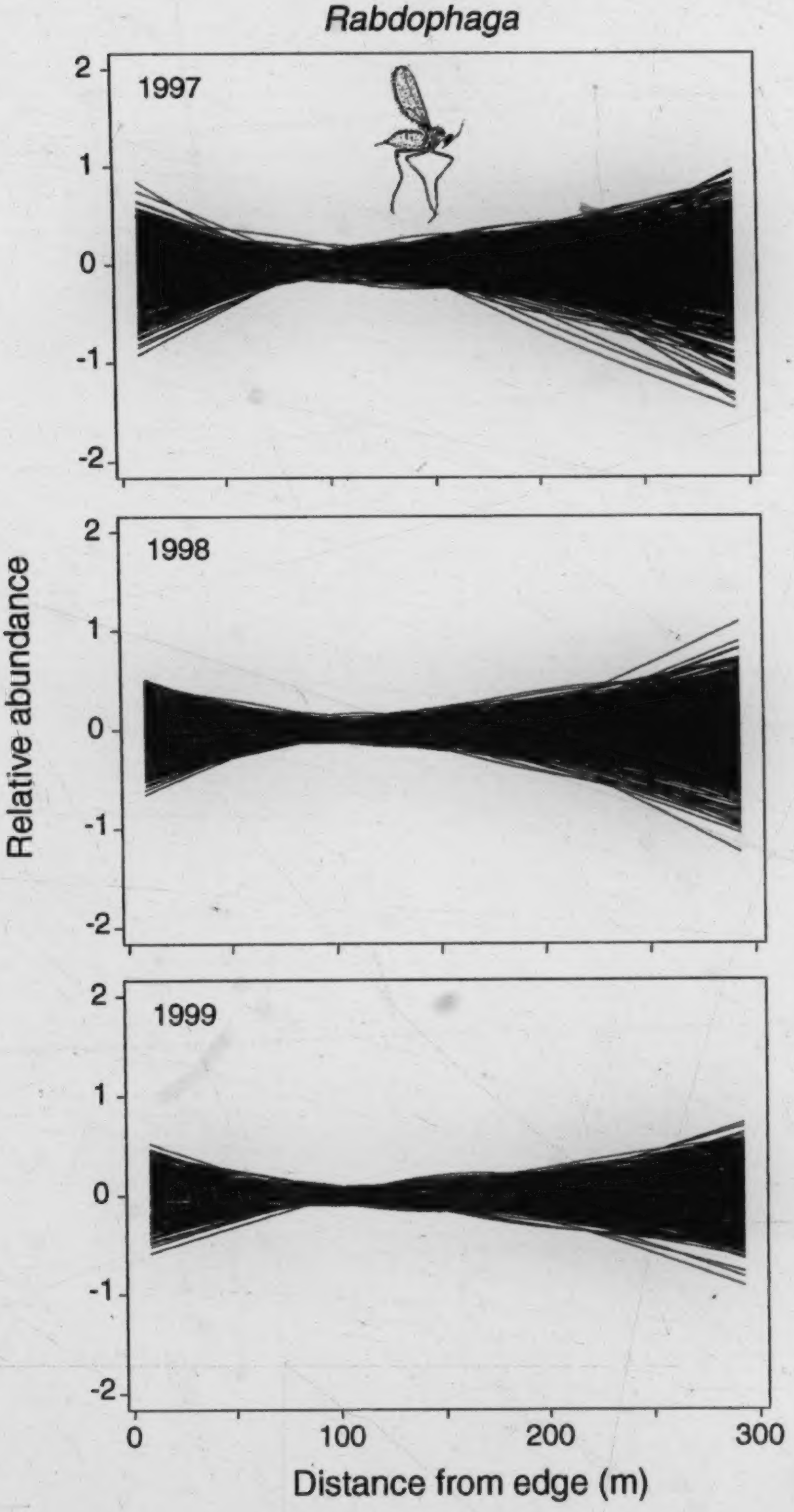

Rabdophaga
1997
1998
1999
Relative abundance
2
1
0
-1
-2
0
100
200
300
Distance from edge (m)

Figure 4-5. Relative abundance of *Gastrancistrus* sp. as a function of the distance to the edge of the cleared area. The observed distribution (solid black line) was determined by fitting a nonparametric cubic B-spline to incidences of parasitised galls on individual willows using a generalised additive model. Grey lines represent functions generated by assuming randomly distributed *Gastrancistrus* among galls.

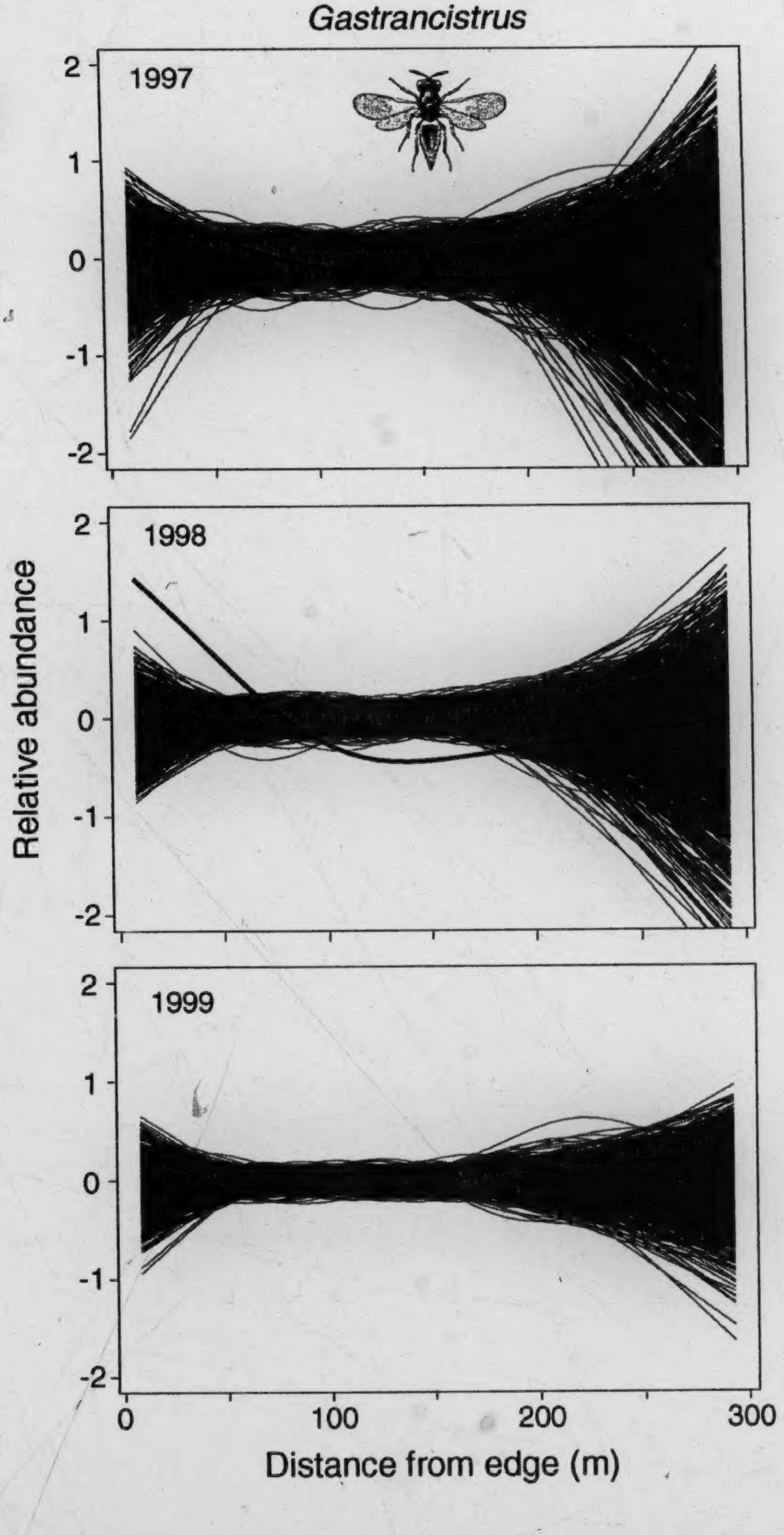

Gastrancistrus
1997
1998
1999
Relative abundance
2
1
0
-1
-2
0
100
200
300
Distance from edge (m)

Figure 4-6. Relative abundance of *Torymus cecidomyiae* as a function of the distance to the edge of the cleared area. The observed distribution (solid black line) was determined by fitting a nonparametric cubic B-spline to incidences of parasitised galls on individual willows using a generalised additive model. Grey lines represent functions generated by assuming randomly distributed *Torymus* among galls.

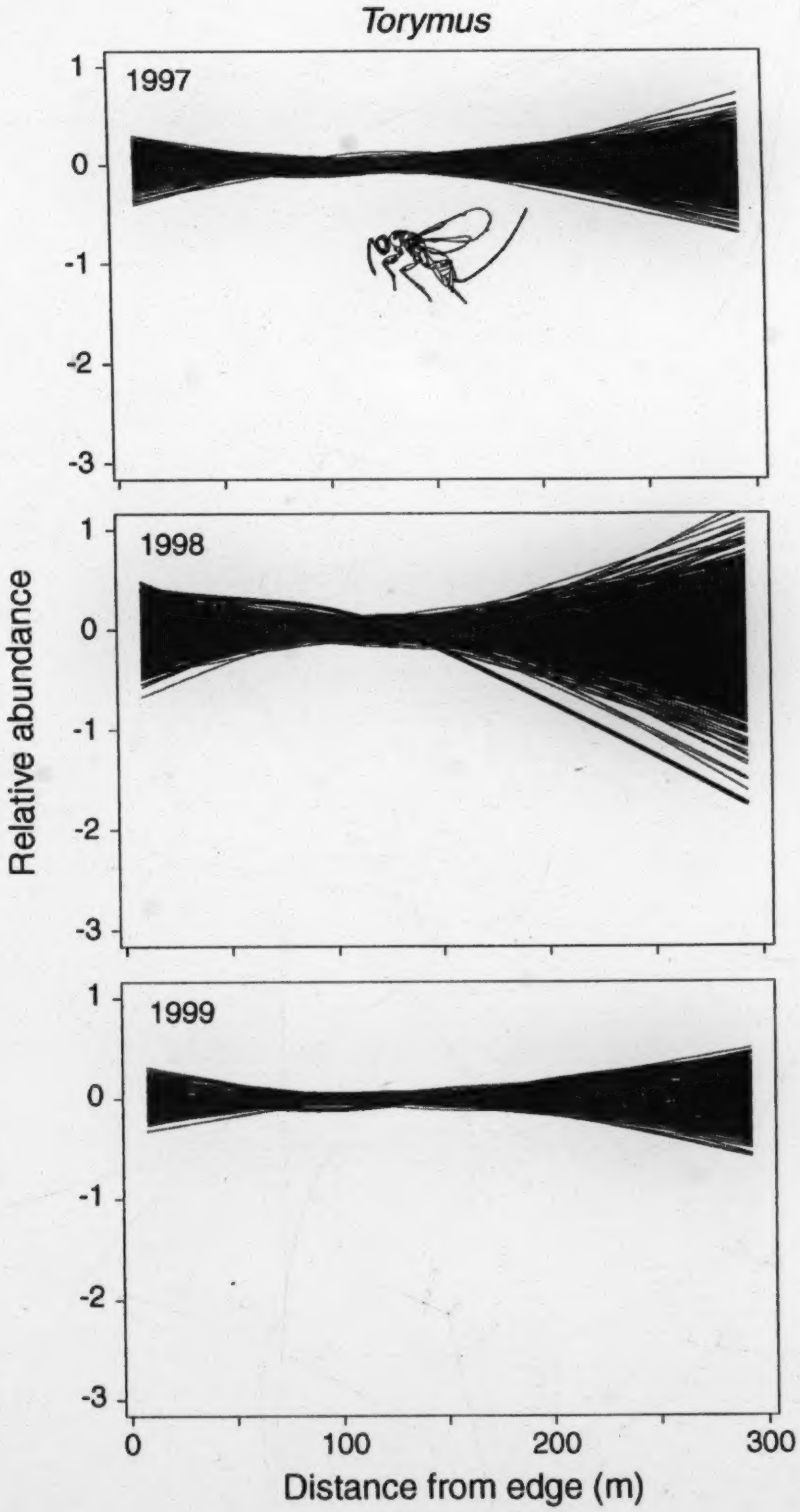

Torymus
1997
1998
1999
Relative abundance
1
0
-1
-2
-3
0
100
200
300
Distance from edge (m)

Figure 4-7. Simulated rates of multiparasitism (M) as affected by differences in the dispersal patterns of *Torymus* and *Gastrancistrus*. Each panel represents a different dispersal pattern for the dominant competitor *Torymus*. Lines within panels represent different proportions of *Gastrancistrus* emigrating from natal willows (μ_{Gast}). The abscissa in each panel indicates the strength of the effect of distance (δ_{Gast}) in reducing the number of *Gastrancistrus* dispersing between patches. Large values of δ_{Gast} correspond to more local dispersal.

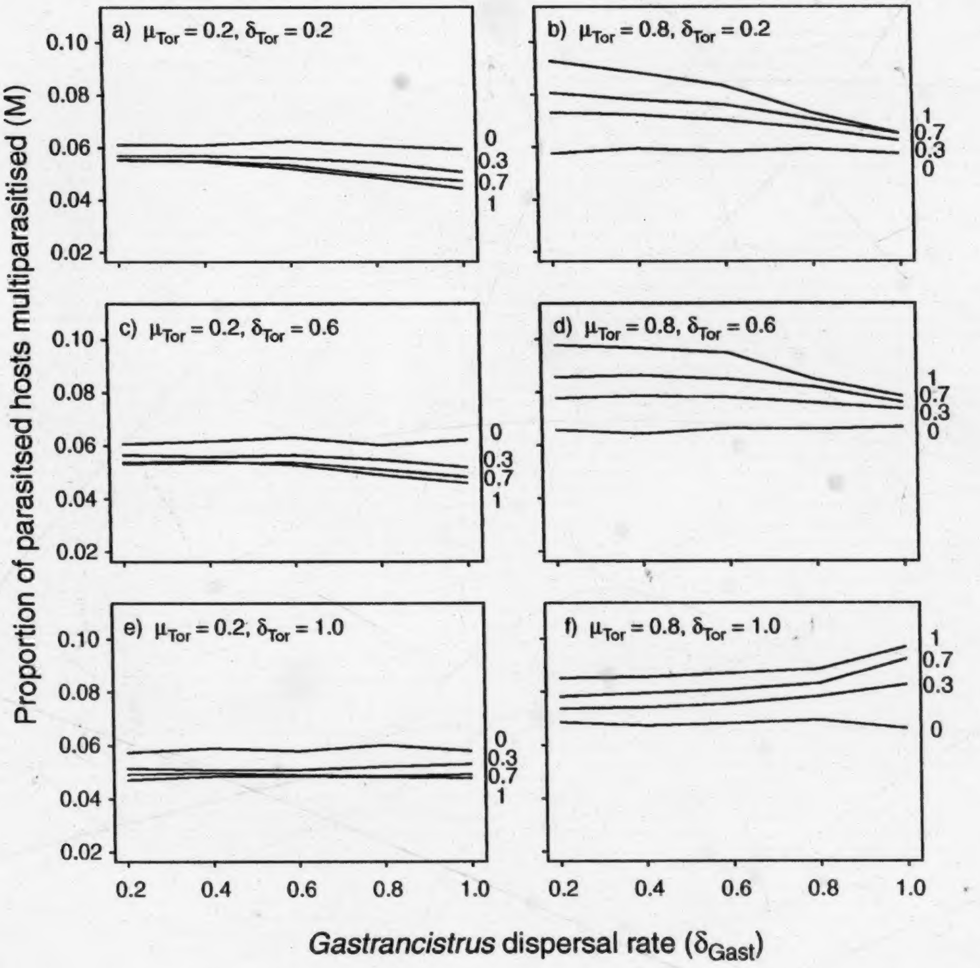

Proportion of parasitsed hosts multiparasitised (M)
a) $\mu_{Tor} = 0.2$, $\delta_{Tor} = 0.2$
b) $\mu_{Tor} = 0.8$, $\delta_{Tor} = 0.2$
c) $\mu_{Tor} = 0.2$, $\delta_{Tor} = 0.6$
d) $\mu_{Tor} = 0.8$, $\delta_{Tor} = 0.6$
e) $\mu_{Tor} = 0.2$, $\delta_{Tor} = 1.0$
f) $\mu_{Tor} = 0.8$, $\delta_{Tor} = 1.0$
0.10
0.08
0.06
0.04
0.02
0
0.3
0.7
1
0.2
0.4
0.6
0.8
1.0
Gastrancistrus dispersal rate (δ_{Gast})

Figure 4-8. The effect of temporal correlation (r) in mean gall diameter on the mean number of generations that *Torymus* and *Gastrancistrus* coexist in a simulated patch network. All simulations were ended after 200 generations.

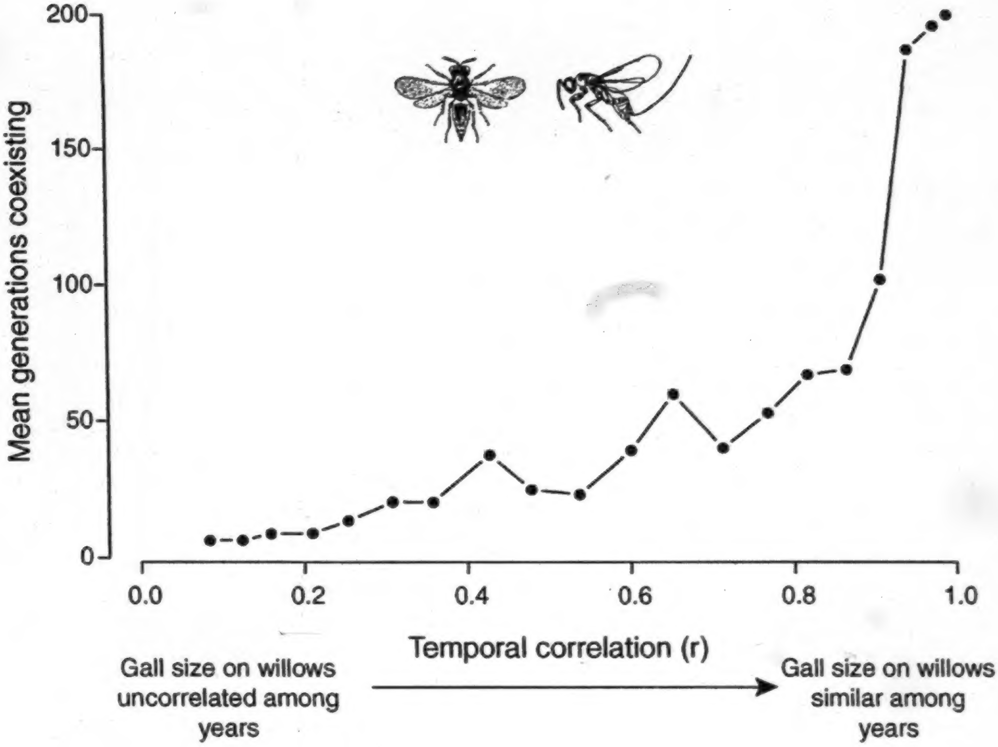
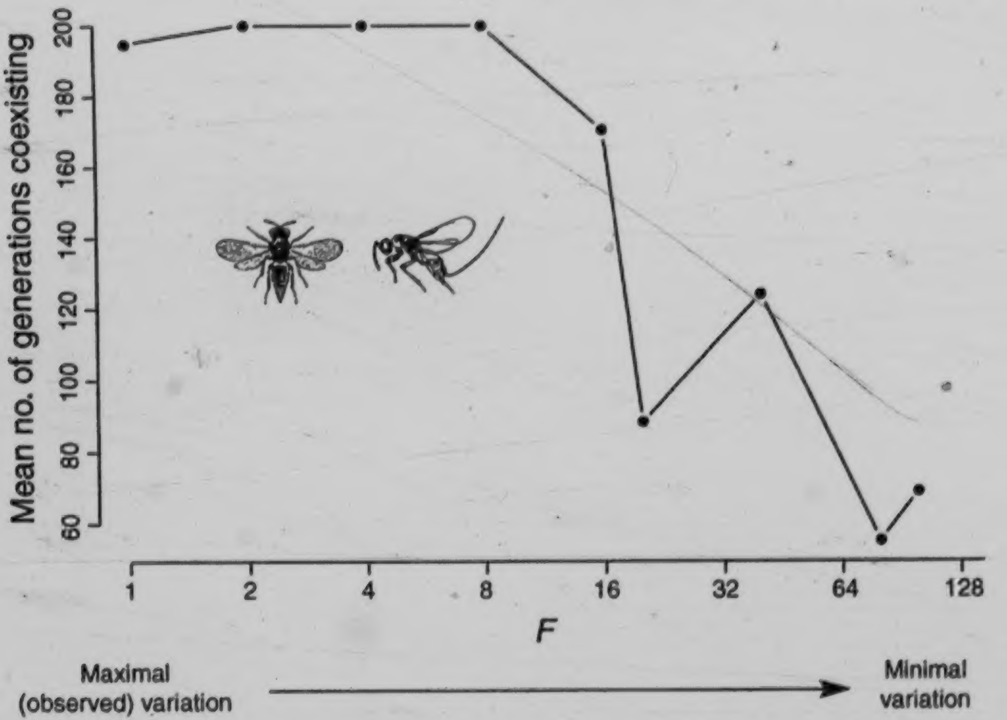

200
150
100
50
0
Mean generations coexisting
0.0
0.2
0.4
0.6
0.8
1.0
Temporal correlation (r)
Gall size on willows uncorrelated among years
Gall size on willows similar among years

Figure 4-9. The effect of spatial variability of refuges (F), and the mean number of generations that *Torymus* and *Gastrancistrus* were observed to coexist in a simulated patch network. Larger values of F correspond to larger-scale variability in refuges caused by a decrease in the response of parasitoids to variation in gall size (see Fig. 4-2). All simulations were ended after 200 generations


Mean no. of generations coexisting
200
180
160
140
120
100
80
60
1
2
4
8
16
32
64
128
F
Maximal
(observed) variation
Minimal
variation

APPENDIX 4-A

Algorithm for generating serially correlated observations from a sample distribution.

From a distribution of uncorrelated observations (A, Box A1), generate a second set of observations (B) by sampling with replacement from the original set. This procedure creates a randomised instance of the original distribution with the same statistical properties. This set is then sorted (C). A reflected image of this set is then appended to both the beginning and end of set D to produce (D). Lastly, another series is generated by shuffling the individual numbers of the sorted series such that their positions only move a limited distance (E). This creates a series of numbers that are similar to, but not the same as, the sorted series. A second run of the algorithm produces another vector (F) which is correlated with set E. By varying the amount of shuffling, the correlation between the set E and set F is also varied, but both maintain the statistical properties of the original distribution of gall sizes.

```
CorResamp_function(sampLen,sampdist){

## S-plus 2000 function
## This function resamples from the vector of sampdist such that multiple
## calls to the function will produce correlated vectors. The resampled
## vectors are still partially ordered so they should be permuted after
## creation (using the same permutation each time to preserve the
correlation).
## The parameter 'sampLen' is a value between 1 and S specifying the half
the
## width of the reshuffling window which determines the amount of
correlation
## between the two vectors.

S_length(sampdist)
startGS_sample(sampdist,S,replace=T)

startGS_sort(startGS)
startGS_c(rev(startGS),startGS,rev(startGS))
OS_round(runif(S,0,sampLen))
negvec_(sample(c(-1,1),S,replace=T))
out_startGS[ c((S+1):(2*S))+(OS*negvec) ]
out

}
```

```
                  91 86 14 64 73  2 94 15 69 80                          (A)
                   2  2 80 91 86 80 86 64 69 91                          (B)
                   2  2 64 69 80 80 86 86 91 91                          (C)

91 … 69 64  2  2   2  2 64 69 80 80 86 86 91 91 91 91 86 86 … 2          (D)

                   0 -2 -2  3  1 -2  3  0  2  1    (vector of position shifts)
                   2  2  2 86 80 69 91 86 91 91                          (E)

                   1 -2 -1  2  0  2  1 -2 -1 -2    (vector of position shifts)
                   2  2  2 80 80 86 86 80 86 86                          (F)
```

Box A1: Example output from the function 'CorResamp' where the original distribution (A) is a uniformly distributed random vector of integers between 1 and 100. The parameter sampLen was set to 3, which corresponds to a high degree of correlation for most distributions.

Chapter 5:
General Discussion and Conclusions

In the past decade the study of host-parasitoid dynamics has seen a rapid inclusion and proliferation of spatially explicit theory, but the empirical support remains impoverished. It is still unclear to what extent spatial processes such as habitat-mediated dispersal underlie spatial or temporal patterns of abundances. This thesis is an attempt to reconcile observed spatial and temporal patterns of abundance in a natural host-parasitoid community with existing theories describing population processes within and among habitat patches. This is done through a combination of experimentation, statistical analysis, and numerical simulation.

Throughout this investigation, the unifying theme has been the close interactions between the species studied in this community, a feature that might be expected when all species come into contact within the space of one cubic centimetre. The galls are the arenas in which these interactions occur and gall size is controlled, in part, by the willow. I found that approximately a third of the variation in gall size among willows can be attributed to the willow's phenotype (Table 2-2) and others have found that the genotype of both the plant and the galling insect affect gall size (Weis & Abrahamson 1986; Weis, Wolfe & Gorman 1989). Both the parasitoids and the predators of *R. strobiloides* respond dramatically and dynamically to variation in gall size (Chapter 2). Furthermore, because the natural enemies attack midge larvae sequentially, and because later attacking species are competitively dominant, the patterns of attack with respect to gall size have a major impact on parasitoid survival. In Chapters 3 and 4, I found that the species interact at spatial scales beyond the patch level. Dispersal between patches is influenced by the spatial distribution of patches and by the type of intervening habitat. The observed differences in dispersal rates may be adaptations to differing distributions of resources or to spatial variation in mortality risk caused by variation in gall size. However, it seems that both spatial and temporal variation in gall size are more important for promoting the coexistence of competing parasitoids and increasing the stability of this host-parasitoid community (Chapter 4).

The importance of gall size for hosts and parasitoids

The results of Chapter 2 convincingly show that gall size is an important factor influencing the overall survival of *Rabdophaga strobiloides* and that it also determines the type of mortality the midge larvae experience. Based on this finding it was clear that gall size would have to be considered as a covariate in all subsequent analyses of the population data. In general this made the population models developed here much too complex for analytical treatment. However, at the expense of generality, this complexity provided the realism necessary for uncovering important patterns that would have otherwise been obscured by unexplained variation or misinterpreted due to the introduction of biases in the estimation of model parameters.

Gall size is an easily measured and obvious characteristic that affects the mortality rates of *R. strobiloides*, and ultimately the dynamics of the entire community. But this trait should be thought of more generally as any host attribute that simultaneously affects a host's risk of mortality and the distribution or quality of a parasitoid's resources. In the studies presented here, I have formulated the host-parasitoid models (both statistical and simulation) such that gall size measurements are incorporated as a factor that modifies a host's (or a parasitoid's) probability of being successfully attacked by another species.. By doing so, any measurable factor that may alter host survival or parasitoid attack probabilities can be easily incorporated into the framework developed here. For example, there are many cases where rates of parasitism are affected by which plant species or on which part of the plant the host feeds (reviewed by Price *et al*. 1980) and many parasitoids respond specifically to host host-plant chemical complexes (Vet & Dicke 1992, Mondor & Roland 1997). These variable, but predictable patterns of host susceptibility can be substituted directly for gall size in the models. In principle, factors that affect susceptibility to parasitism or predation can be described by models of heterogeneity of risk, but that class of models generally employs well defined probability functions and is less amenable to the diverse assortment of risk functions which are typical of empirical studies.

Many physiological and behavioural characteristics of insects can influence their chances of being attacked by a parasitoid or predator. A large number of species of herbivorous diptera and lepidoptera are concealed within plant tissue during one or more life stages, and in most cases it is likely that this adaptation results in more than one benefit to the insect (Price, Fernandes & Waring 1987). Because the evolutionary history of *R. strobiloides* is unknown, it is impossible to know the factors that led to its galling habit. It is clear however, that increased gall size confers a substantial survival advantage for *R. strobiloides* (Fig. 2-1). The selection intensities, which are a measure of the selective advantage of a particular trait (Falconer 1981), were found to range between 0.37 and 0.52 for the five cohorts for which we could measure overall survival in the two study areas, and in all of these cohorts, the highest survival was consistently in the largest gall-size classes. The magnitude of these values, and the shape of the survival functions (Fig. 2-1), compare well with those observed for *Eurosta solidaginis* galls in Pennsylvania (Weis, Abrahamson & Andersen 1992) but are significantly higher than that observed for *Euura lasiolepis* galls in Arizona (Price and Clancy 1986). The differing intensities might simply be attributable to difference in the composition of species in the community of natural enemies.

From the perspective of the parasitoids, gall size has two important implications. First, it is an important attribute governing the distribution and availability of hosts, and second, it can also confer protection from other natural enemies attacking later in the season. It appears that *Gastrancistrus* is able to attack galls that eventually exhibit a wide range of diameters but has a much greater chance of surviving to the adult stage when it attacks galls that become large (Fig. 2-4). It is unclear from this work if *Gastrancistrus* selects these galls for oviposition or if this koinobiont manipulates its host to produce a larger gall for its own benefit. Further work involving manipulative experiments should be done to examine this issue more thoroughly such as the study by Plantard, Rasplus & Hochberg (1996).

Torymus appears to specialise on the most abundant size classes to the exclusion of very small and very large galls. This strategy is likely shaped by constraints on ovipositor length in the largest galls (>20 mm diameter) and high rates of predation by birds on the smallest galls (< 7 mm, Fig. 2-2). Because of these constraints on attack, upward shifts in average gall size or in the size distribution of bird attacks may negatively affect the host availability or survivorship of *Torymus*. Weis, McCrea & Abrahamson (1989) found through simulations that if the parasitoid's ovipositor length is related to the size of its natal gall, then the population of parasitoids could respond phenotypically to increasing average gall diameter. However, for *R. strobiloides* and *T. cecidomyiae* it is unknown how well parasitoid ovipositor length is correlated with host and gall size and further work should be done to define this relationship.

Measuring host and parasitoid dispersal

Empirical tests of spatially explicit host-parasitoid theory have been severely hampered by the difficulties involved with quantifying the movement of very small animals (Godfray 1994). Two approaches are typically used to measure dispersal. In the first, the geographic expansion of alien pests, or parasitoids introduced for their control, is measured. In the second, individuals are marked using various techniques and then recaptured after moving some distance.

Dispersal estimates based on novel introductions of insects and their subsequent expansion vary widely from 0.16 km per year for a whitefly parasitoid (Onillon 1990) to 160 km per year (DeBach 1974) for a tachinid fly. There are several major problems associated with these dispersal estimates and others collected in a similar manner. First, these studies typically indicate only the maximum range of colonisation and give little indication of the shape of the dispersal curve or even how far most of the individuals travel during their lifetimes. It is this latter type of information that is most relevant to much of the spatial theory (Hassell 2000). Secondly, there have been no studies relating expansion rates of insects into unoccupied habitat, to rates of dispersal in endemic populations. In most cases, the direction, shape and strength of this relationship will likely depend on the details of the insect's reproductive physiology and its behaviour when encountering empty or occupied habitat. Lastly, little or no information on the abundance or distribution of the insect's limiting resource (host plants, host insects or specialised habitats) is available, and this factor may have a major impact on a species' ability to spread throughout a region.

In a study using individually marked hosts and parasitoids, Jones, Godfray & Hassell (1996) found that four species of parasitoids had daily movement rates between 5 and 30 m and that most females lived less than 10 days. However, they confined their recapture effort to an area of approximately 2000 m^2 with a maximum dimension of approximately 50 m. This drastic restriction on the recapture area is typical of mark-release-recapture studies and can severely bias estimates of dispersal rates (Turchin

1998). In another study of host and parasitoid dispersal utilising marks, Dempster *et al.* (1995) found that tephritid hosts tended to move widely between patches (up to 2km), but little could be said concerning parasitoid movement since only a very small proportion of marked individuals were recaptured exemplifying another typical problem with estimating dispersal in this way.

The techniques for estimating dispersal rates developed in this study (Chapter 3) provide a valuable alternative to the previously discussed methods and overcome some of their weaknesses. First of all, the data required for estimation can come from censuses of endemic populations of hosts and parasitoids or alternatively from populations expanding into unoccupied habitat. However, there is the constraint that there must be sufficient spatial heterogeneity in population densities such that the 'dispersal signal' can be detected against the background of noise. Second, because local population parameters (such as host growth rate and parasitoid searching efficiencies) and dispersal rates are estimated simultaneously, biases caused by ignoring one or the other factor will be minimised (Lele, Taper & Gage 1998). For example, estimation of the host's population growth rate is particularly prone to bias caused by dispersal. The modelling approach used here reduces bias in the estimation of density dependent growth rates if dispersal is density independent, but does not presently consider the potentially confounding effects of density dependent dispersal. The effects of this type of dispersal on spatial dynamics have recently been explored by French & Travis (2001) using simulations, but it is unclear if the associated parameters would be identifiable in a statistical analysis of field data. A third advantage of this approach is that spatially explicit simulations can be easily conducted because the parameterised model incorporates key within and between-patch processes. These simulations can be used to make short- term population forecasts or to explore long-term stability properties of the communities.

The role of dispersal in the dynamics of the willow pinecone gall community

In Chapter 3, using population census data, I found that the midge dispersed less than the two parasitoid species and that the parasitoids tended to disperse equally well throughout the study site. The results of the removal experiment in Chapter 4 as well the analyses of patch colonisation rates, suggest that the midge is the best coloniser of vacant habitat and that the parasitoids had lower colonisation abilities. In part, this discrepancy can be attributed to differences between the two techniques in their sensitivity to detecting long-range movements.

The discrepancy may also be attributed to differences in the behavioural responses of the insects encountering empty versus occupied habitat. In many parasitoid species, it is known that females will alter their movement rates in response to the presence of conspecifics or their chemical odours (Price 1970, 1972, Vinson 1972, Greany & Oatman 1972, van Dijkken et al. 1992). Increased conspecific encounter rates tend to increase the probability of leaving a patch (van Lenteren 1981,1991, Haccou *et al.* 1991) or decrease the number of progeny allocated to a patch. Conversely, an increased rate of encounter with unparasitised hosts, or similarly a high host-to-parasitoid ratio, tends to promote patch residency and increased progeny allocation

(Waage 1978, van Alphen & Galis 1983, French & Travis 2001). If similar behaviours occur in the species I studied, I would expect that parasitoid movement rates through occupied habitat (as measured by the distribution of progeny) would be greater than in unoccupied habitat.

The removal experiment (Chapter 4) clearly showed that the three species are able to colonise relatively large areas of vacant habitat, but do so at different rates. However, it is not known what are the ultimate mechanisms shaping these colonisation patterns or how relevant these differences are to the ecology of each species, and to the ecology of the community as a whole. Presently, Bebb's willow is a widespread and common component of the vegetation in Alberta's parkland ecoregion (Moss 1983), and at the Rumsey Ecological Reserve, willows can be more than 100 years old and still support gall development (personal observation). Furthermore, natural enemies do not cause widespread reductions in gall densities as was found in an oak-galling cynipid (Washburn & Cornell 1981). Therefore, large areas of vacant habitat may be a rare situation encountered by the species in this community. If this is the case, a long-range dispersal strategy would provide little benefit. Fires or widespread climatic events have the potential to create large areas of vacant habitat but it is unknown how frequent, or to what extent, such events occur over the range of *R. strobiloides* in Alberta.

If the present situation (common and widespread habitat patches) is typical of the evolutionary and ecological environment of *R. strobiloides* and its parasitoids, the results from the growth-dispersal model (Chapter 3) are a more likely depiction of the dispersal strategy employed by the gall midge. Using the best-fitting model (Table 3-2, Model 6) it was estimated that approximately 75% of a midge's reproductive effort is allocated to its natal bush and that dispersal is typically limited to less than 40 m. For most willows in the study area, this distance would encompass many suitable patches and even more numerous suitable oviposition sites. This oviposition strategy would allow some of a female's eggs to develop on a suitable willow (the one on which she developed), as well as ensuring that not all of her progeny died due to infrequent stochastic events at her natal patch.

The distribution of resources on which the parasitoids depend is defined by the subset of willows that support galls, and is further limited by the subset of galls that are suitable for attack (due to gall size effects). Given this more scattered distribution of resources, I would expect parasitoids to have greater dispersal capabilities than their host. This is consistent with the estimates obtained in Chapter 3. In general, the patterns of colonisation-by-isolation in Chapter 4 suggest that differential dispersal patterns may promote the coexistence of the two parasitoid species. However, the results of the parameterised simulations suggest that spatial and temporal variability in gall size that has a larger effect on coexistence.

Summary

This thesis is the first empirical challenge of spatially explicit host-parasitoid models in a natural community. Intensive observations on the fates of individual *R.*

strobiloides larvae revealed that gall diameter strongly affects larval fitness and that it structures the host availability and survival of the parasitoids *Torymus* and *Gastrancistrus*. Using the framework of existing spatial host-parasitoid models, and extending these to include gall-size induced refuges, it was found that the dispersal patterns of hosts and parasitoids could be successfully estimated using spatial population data. However, community dynamics were best explained by refuges resulting from spatial and temporal variation in gall size and not by differential dispersal among patches. These findings suggest that spatial patterns of abundance of hosts and parasitoids predominantly result from local mechanisms and that dispersal-induced spatial patterns are relatively unimportant in this community.

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Appendix A: Identifying Gall Fates

A significant advantage of using gall-forming insects for studying the dynamics of populations is that the past history of each individual is written in the structures and characteristics of the gall. This feature is particularly useful if the populations exist at low densities and the sampling of live individuals would substantially alter those densities. For this thesis I identified a suite of characters based on mature galls that could be used to diagnose the fate of a gall midge during its larval and pupal stages. This was done by collecting mature galls approximately two weeks prior to insect emergence and placing them individually in 12 dram plastic snap-cap vial with vented lids. These vials were then kept at room temperature to allow normal emergence of either the host insect (*Rabdophaga strobiloides*) or its parasitoids. After emergence, galls were carefully dissected to associate characters of the gall with the species of insect that emerged from that gall. In cases where no insects emerged from a gall, the fate of the gall midge was described based on my knowledge of the growth patterns of the galls and other sources of mortality that were commonly encountered. The result of this method is presented below as a diagnostic key.

KEY TO FATES OF *RABDOPHAGA STROBILOIDES* LARVAE

1a. Larval chamber well formed; outer scales of gall may be damaged on one side often extending to gall center..2

1b. Larval chamber not formed or not evident due to significant damage in the center of the gall 6

2a. Circular exit hole in side or top of larval chamber and/or chamber contains gall fibres 3

2b. No exit hole in larval chamber 4

3a. Dark grey, meconial pellet in the base of larval chamber; bracts growing from floor of chamber; gall material in chamber shaped as distinct pellets not long fibres; silk lining of chamber often not evident...................................... .... **Parasitism by *Torymus cecidomyiae***

3b. No meconial pellet in chamber; floor of chamber smooth concave; gall material in chamber shaped as long fibres; silk lining of chamber usually evident..**Parasitism by *Gastrancistrus* sp.**

3c. No meconial pellet in chamber; floor of chamber smooth concave; gall material in chamber shaped as large pellets; silk lining of chamber usually evident..**Parasitism by Encyrtidae**

4a. Larval chamber empty..5

4b. Larval chamber contains pupal case formed from the integument of third instar *R. strobiloides* larva ....**Parasitism by *Platgastridae***

5a. Significant damage to outer scales extending to center.........**Bird predation**

5b. No damage to gall; larval chamber lined with silk................................ ....Successful emergence of *R. strobiloides*.

6a. Larval chamber not formed ....**Failed gall**

6b. Larval chamber not evident due to significant damage ;frass present........... ....**Lepidopteran feeding**